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A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America

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A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America

C. P. NUTTALL

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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SYNOPSIS. Non-marine Tertiary molluscan faunas of Colombia, Ecuador and the 'Pebasian' of the Upper Amazon Basin of eastern Peru and adjoining parts of Brazil are reviewed, and compared with the living fauna of South America. New Colombian fossil faunas from La Tagua, on Rio Caqueta, and Puerto Nariño, on Rio Marañón, are described: the latter is Pebasian. The new La Tagua fauna provides a valuable link, permitting correlation between the Santa Teresa (San Juan de Rio Seco of Anderson, 1928), La Cira (both Magdalena Valley) and Pebasian faunas.

All are thought to be Miocene: the Pebasian, the only one in which living species (of Hemisininae and *Mytilopsis*) occur, may be the youngest. Some faunas, mainly from the Rio Jurua region of Brazil, strongly resemble those of the present day and are considered to be post-Pebasian. The Mugrosa fauna (Magdalena Valley), now reduced to two species one of which occurs in the La Cira, is, if not Miocene, unlikely to be much older. The earliest Magdalena Valley fauna is the Los Corros, which may be late Eocene or early Oligocene and has very little in common with the overlying Mugrosa and La Cira. Faunas from the intermontane basins of Ecuador, including the rich Loyola and Mangán of Cuenca Basin, are accepted as Miocene, following Bristow & Parodiz (1982).

Modifications are proposed to the hypothesis of Kätzer (1903), who suggested that during the Tertiary the Upper Amazon area was occupied by an inland sedimentary basin connected to the sea by the Marañón Portal lying to the south of the Bay of Guayaquil. Evidence is presented that during the mid-Tertiary a brackish water connection existed between the Upper Amazon Valley and the Caribbean by a north–south trough, lying parallel to the still rising Andes and occupied by a continually shifting pattern of streams, swamps and lakes of varying salinity. Similarities between the La Cira and Santa Teresa faunas of the Magdalena Valley and those of La Tagua demonstrate that they were all deposited before the Andean orogeny at the close of the Miocene raised the Cordillera Oriental to form a mountain barrier impenetrable to aquatic molluscs between the Magdalena and Upper Amazon Valleys. There is also some palaeontological evidence for fresh (not brackish) water connections from the Pebasian Basin, running eastwards down the present Amazon Valley between the Guiana and Brazilian Shields and southwards towards the estuary of Rio de la Plata.

Taxonomic conclusions include the following. *Eubora, Tropidobora* and *Toxosoma* are now assigned to the Lithoglyphinae (Rissoacea, Hydrobiidae). *Nanivitrea* is the first representative of the Cochliopinae (Hydrobiidae) to be recognized fossil in South America. Vitrinellidae (Rissoacea) are recognized in the Pebasian, the first known non-marine occurrence of the family. At least one species is thought to be lecithotrophic, the first record of this mode of development in the family. The Mutelacea are distinguished from the Unionacea by their coarser prismatic shell layer. *Ostomya*, which may share common ancestry with *Guianadesma*, is redescribed and transferred from the Lyonsiidae to the Corbulidae.

The following new taxa are described. Gastropoda: Rissoacea, Hydrobiidae, *Dyris hauxwelli, D. semituberculata, Liris acicularis* (Littoridininae); *Nanivitrea colombiana* (Cochliopinae); Vitrinellidae, *Vitrinella (Vitrinellops) hauxwelli, V. (V.) degrevei*; Cerithiacea, Thiaridae, *Sheppardiconcha lataguensis, Longiverena colombiana* and *Verena lataguensis*. Bivalvia, Corbulidae, *Pachydon ovalis, P. trigonalis* and the genus *Pebasia* (type species *Pachydon dispar* Conrad), which probably shares common ancestry with *Pachydon*.

Lectotypes of the following nominal species are selected. Gastropods: *Aylacostoma tuberculata* Spix, 1827; *Cerithium coronatum* Etheridge, 1879; *Dyris gracilis* Conrad, 1871; *Hemisinus behni* Reeve, 1860; *H. eucosmius* Pilsbry & Olsson, 1935; *H. hopkinsi* P. & O., 1935; *H. lapazanus* P. & O., 1935; *H. obesus* Reeve, 1860; *H. olivaceus* Reeve, 1860; *H. pulcher* Reeve, 1860; *H. punctatus* Reeve, 1860; *H. tenellus* Reeve, 1860; *H. tenuilabris* Reeve, 1860; *H. zebra* Reeve, 1860; *H. (Verena) avus* Pilsbry & Olsson 1935; *H. (V.) laevicarinata* P. & O., 1935; *Liris laqueata* Conrad, 1871; *Melania bicarinata* Etheridge, 1879; *M. nicotiana* Reeve, 1860; *M. scalarioiodes* Etheridge, 1879; *M. venezuelensis* Reeve, 1859; *Neretina puncta* Etheridge, 1879; *N. ziczac* Etheridge, 1879; *Strombus lineolatus* Wood, 1828; *Turbonilla minuscula* Gabb, 1869. Bivalves: *Anisothyris (Pachydon) tumida* Etheridge, 1879; *Corbula abundans* Pilsbry & Olsson, 1935; *C. canamaensis* Etheridge, 1879; *C. hettneri* Anderson, 1928; *C. magdalensis* Pilsbry & Olsson, 1935; *Dreissensia dalli* Clerc, *in* Joukowsky & Clerc 1906; *Pachydon cuneatus* Conrad, 1871; *P. dispar* Conrad, 1874.

INTRODUCTION

This work is a partial revision of the Tertiary non-marine molluscan faunas of the north-western quadrant of South America, bounded approximately by 10° S and 60° W. It is concerned with their systematic descriptions, and also their stratigraphical and palaeogeographical implications. When considering these latter aspects, it must be borne in mind that these non-marine fossiliferous horizons seldom exceed ten metres in thickness, but occur in basins where as much as 10,000 m of sediment have accumulated during the Tertiary (Campbell & Bürgl 1965: 581). Much of this thickness may have been deposited very rapidly following uplift during mountain-building phases, whilst the fossiliferous bands may represent comparatively quiet periods, with slow deposition of lake and other fresh-water sediments. Nevertheless, it is more than likely that the non-marine molluscan fossil record accounts for only a tiny percentage of Tertiary time. In addition, the various periods of mountain-building will have greatly changed the geography of the region since the fossiliferous sequences were deposited. At the present day, in the Amazon Valley such beds lie at well under 300 m above sea level, whilst at the other extreme, the not necessarily contemporaneous deposits of the intermontane basins of Ecuador (Cuenca etc.) lie at altitudes of between 2,500 and 3,500 m. Furthermore, uplift has caused relative vertical movements of approximately 8,000 m in the base of the Tertiary in the Eastern Cordillera of the Colombian Andes (Campbell & Bürgl 1965: 567).

The study was primarily concerned with newly collected faunas from La Tagua on the Rio Caqueta, Colombia, and their relationship with similar, but by no means identical, faunas from some 500 km further south in the Pebasian Basin of the Upper Amazon in Peru. It does not deal in any detail with taxa which are unimportant in these faunas: thus the Corbiculacea are omitted and the Naiades (Unionacea and Mutelacea) are treated comparatively briefly. The other faunas upon which the work concentrates are from the Magdalena Valley in Colombia and those from the intermontane basins of Ecuador. In addition, a search has been made of both Tertiary and Recent faunas, in particular of Central America and the Caribbean as well as the remainder of South America, for comparable taxa.

Some of the allegedly Palaeogene faunas, described

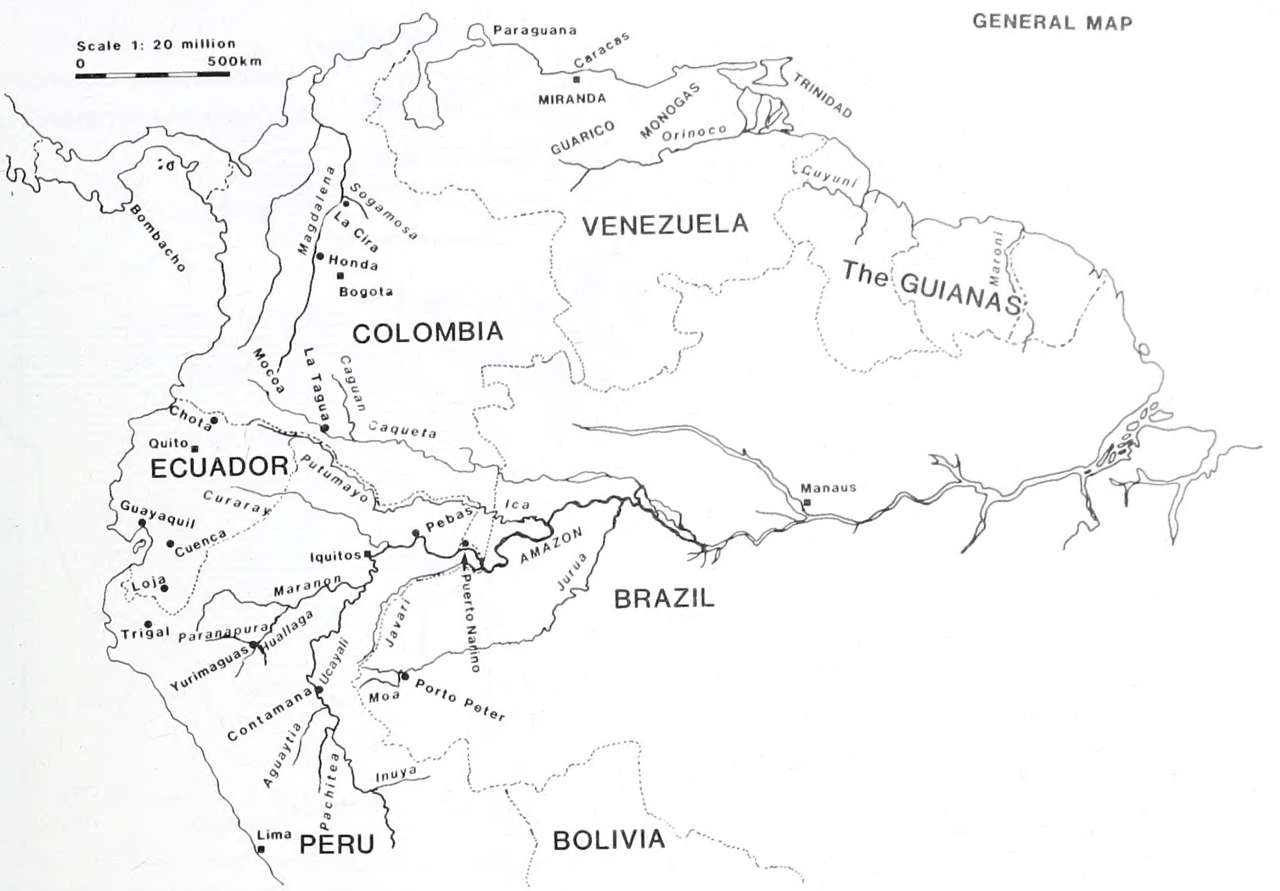
GENERAL MAP
Scale 1: 20 million
0 500km
Paraguana
Caracas
MIRANDA
GUARICO
MONOGAS
Orinoco
TRINIDAD
Cuyuni
VENEZUELA
The GUIANAS
Maroni
Sogamosa
La Cira
Magdalena
Honda
Bogota
COLOMBIA
Bombacho
Mocoa
La Tagua
Caguan
Caqueta
Chota
Quito
ECUADOR
Putumayo
Curaray
Guayaquil
Cuenca
Iquitos
Loja
Maranon
Pebas
Ica
AMAZON
Jurua
Puerto Nariño
Manaus
BRAZIL
Trigal
Paranapura
Huallaga
Yurimaguas
Javari
Ucayali
Contamana
Moa
Porto Peter
Aguaytia
Pachitea
Inuya
Lima
PERU
BOLIVIA

Fig. 1 General Map of northern South America to show principal rivers and most places referred to in the text. See also Figs 4 (p. 172), 443 and 444 (p. 323).

(Anderson 1928, Pilsbry & Olsson 1935) from the Magdalena Valley of Colombia, have proved younger than originally thought, and have species in common with the new faunas from about 500 km further south in the La Tagua region of Colombia, which is now part of the present-day Amazon Valley system. The implication is that these faunas must predate the late Miocene Andean orogeny which raised the Cordillera Oriental now separating the Magdalena Valley from the Upper Amazon Valley of eastern Peru as well as from the Oriente of Ecuador.

The first work dealing with the Amazon Basin Tertiary molluscan faunas was that of Gabb (1869), who described a small fresh- or brackish-water fauna from Pebas on Rio Marañón in eastern Peru. Now known as Pebasian faunas, these proved to be both rich and unusual and were the subject of several papers, mostly written in the 1870s. They have also in the past been termed Iquitosian (Steinmann 1930, unseen; see p. 357), after the particularly rich fauna of Iquitos. In the present work, the term **Pebasian** is used to describe the faunas of the Pebas district, as well as the age of the deposits in which they occur and the basin in which these deposits are found. The fauna of Pebas itself is comparatively poorly known and the exposures there were apparently last examined by Bassler, *c.*1925; his collection was discussed briefly by Willard (1966). Measurements of the sections at Pebas were given by Hartt (1872); details in later papers by other authors are always based on his figures. In these circumstances, the present paper hardly seems to be an appropriate place in which to propose the use of the term 'Pebasian' in a formal sense. It is not, therefore, here recognized as being an established Stage. Costa (1980: 870) introduced the term 'Formação Pebas' informally, followed (1981: 635) by a formal description of the Formation.

Brazilian geologists responsible for the *Projeto Radambrasil* volumes (e.g. del'Arco 1977) have referred the Pebasian faunas to the Solimões Formation. However, their maps show large tracts of Tertiary deposits, stretching as far east as Manaus, as belonging to this formation, and they have also referred to it other faunas, both of vertebrates and of molluscs, more resembling those of the present-day Amazon Valley but having almost nothing in common with those of the Pebasian. The differing opinions held by various authors as to the age of the Pebasian are summarized in the well-illustrated monograph of de Greve (1938: 123), and range from Palaeogene to Pliocene. In recent years, they are generally accepted as probably Pliocene, but in the present study it is recognized that they could well be Miocene. The non-marine molluscan faunas of the Pebasian have been described in several other papers (Woodward 1871, Conrad 1871*b*, 1874a, *b*, Boettger 1878, Etheridge 1879, Roxo 1924). More recent works (Santos & Castro 1967, Costa 1980, 1981, Kadolsky 1980) have been mainly of a revisory nature.

The Pebasian faunas are markedly different from those of the present day (Baker 1914, Haas 1949*a*, *b*, 1950, 1952, 1955), suggesting very different facies. The 'fresh-water mussels', Unionacea and Mutelacea, and river snails of the

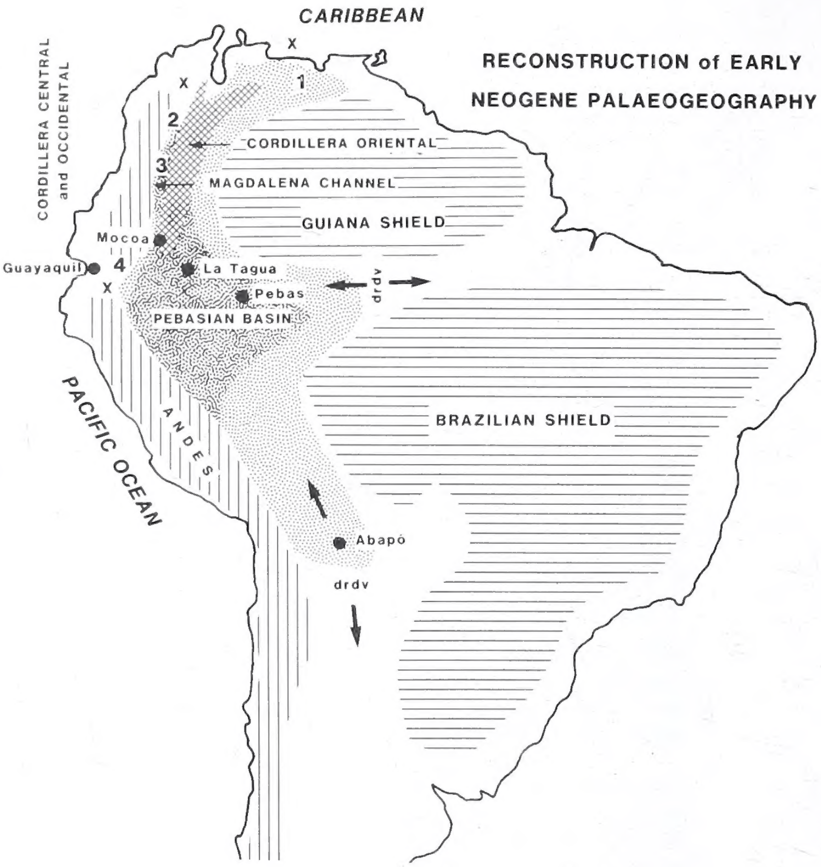

Fig. 2 Reconstruction of early Neogene palaeogeography (See also Fig. 453, p. 351). Key: horizontal lines, ancient massifs; vertical lines, Andes mountains (except for cross-hatched, Cordillera Oriental of Colombian Andes); light stipple, maximum extent of possible brackish water basin; heavy stipple, areas where there is some fossil evidence for the existence of a brackish-water basin; drdv, drainage divides; arrows, direction of river flow; X, possible connections between brackish water basin and sea. Numbers indicate general areas from which other non-marine faunas have been described. 1, northern Venezuela (Palmer 1945; Rutsch 1952; Macsotay 1968); 2, Middle Magdalena Valley (Pilsbry & Olsson 1935); 3, Upper Magdalena Valley (Porta 1966); 4, Cuenca and other intermontane basins of Ecuador (Bristow & Parodiz 1982). *Pachydon* possibly occurred as far south as the Abapó region of Bolivia (p. 344).

South America is shown as an island, predating the formation of the Panama land bridge in the late Neogene. The Cordillera Oriental was raised during Middle and Late Miocene orogenies, and prior to this there would have been no barrier between the Magdalena and Amazon Valleys. During the rise of the Cordillera Oriental, the Magdalena is presumed to have formed a north–south channel whose southern end was eventually closed in the Mocoa region.

Thiaridae are often surprisingly uncommon, whilst all records of the Pleuroceridae appear to be based on misidentifications of Thiaridae. As expected, Hydrobiidae are common, but the genera present in the Pebasian are largely endemic. Among the most striking features of the Pebasian is the presence of the families Neritidae, Corbulidae and Dreissenidae which are now absent from the region and tend to be indicative of at least brackish if not marginal marine conditions. Perhaps the most surprising occurrence is that of Vitrinellidae (Rissoacea), a family with an otherwise entirely marine distribution. The presence of this Pebasian molluscan assemblage in the Upper Amazon Basin has important implications when the palaeogeography of the continent is considered.

One of the features of the present-day topography is the broad strip of comparatively low-lying terrain stretching from the Caribbean to the estuary of the Rio de la Plata, with the Andes lying along its western margin and the Guiana and Brazilian shields to the east. The evidence from both the fossil and Recent distribution patterns of the molluscs points to a connection northward from the Amazon region to the Caribbean during the Tertiary; the presence of identical species in the La Tagua and Magdalena Valley fossil faunas suggest a direct connection between the two areas. From this it follows that they predate the Late Miocene orogeny that raised the Cordillera Oriental of the Colombian Andes, creating a barrier to aquatic molluscs. The fossil faunas of Argentina do not suggest a similar marine to brackish connection from the Upper Amazon to Rio de la Plata. However, some fresh-water Hydrobiidae (Subfamily Lithoglyphinae) now living in the La Plata region appear to be the closest relatives, either fossil or Recent, of the more unusual Pebasian members of the family. No acceptable evidence has been found of a marine east/west migration route during the Tertiary along the course of the present-day Amazon, even though this idea has been recently resurrected by Sheppard & Bate (1980), who described ostracod faunas from the Pebasian and the La Tagua Beds. The possibility of a connection with the Pacific through the so-called Marañón Portal, lying in the Ecuadorian–Peruvian boundary region, was first postulated by Kätzer (1903) and has been espoused by several subsequent authors. Its existence is accepted herein as being likely, but none of the available evidence invalidates the argument in favour of an additional connection northward to the Caribbean.

The present study stemmed from an enquiry for the identification of Tertiary non-marine molluscan fossils found at the completely new Colombian localities at La Tagua, on Rio Caqueta, where it crosses the Equator. The material was collected by the Colombian Amazonas Expedition (CAE), and submitted in 1978 by Michael J. Eden, a geographer of London University. In 1979, Eden forwarded more material collected by Mr Nout Weeda (also CAE), from a different locality near La Tagua which yielded better-preserved material, and from another entirely new locality, Puerto Nariño on the Colombian Amazon, which contained a slightly unusual Pebasian fauna. See p. 172.

The Palaeontology Department of the British Museum (Natural History) (BMPD) already possessed two collections of Pebasian fossils from the Upper Amazon region of Peru. That from Canamá was collected by Brown, who gave an account of the geology (1879). The small fauna was described by Etheridge (1879): unfortunately, much of the material is lost, having apparently never reached the Museum. The other

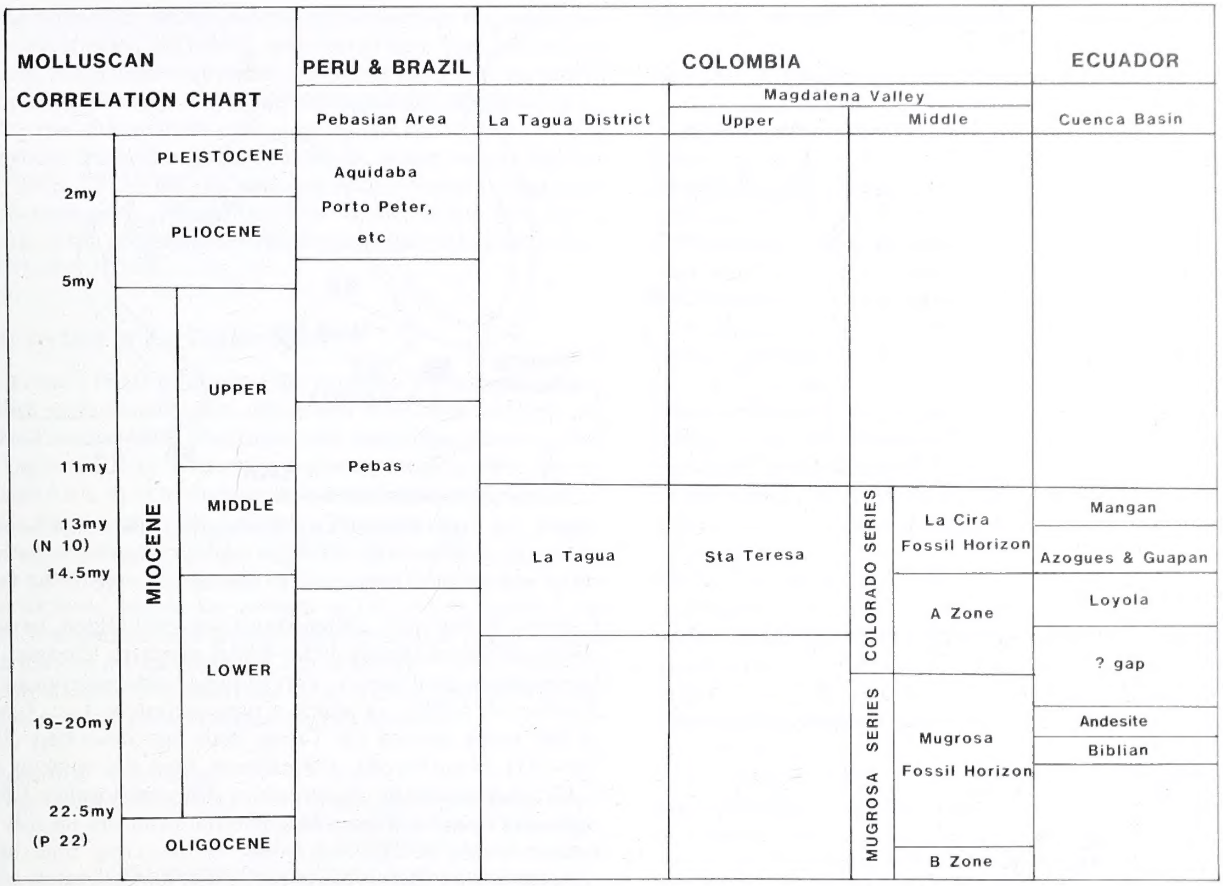
MOLLUSCAN CORRELATION CHART
PERU & BRAZIL
COLOMBIA
ECUADOR
Pebasian Area
La Tagua District
Magdalena Valley
Upper
Middle
Cuenca Basin
PLEISTOCENE
2my
PLIOCENE
5my
MIOCENE
UPPER
11my
MIDDLE
13my
(N 10)
14.5my
LOWER
19-20my
22.5my
(P 22)
OLIGOCENE
Aquidaba
Porto Peter, etc
Pebas
La Tagua
Sta Teresa
COLORADO SERIES
MUGROSA SERIES
La Cira Fossil Horizon
A Zone
Mugrosa Fossil Horizon
B Zone
Mangan
Azogues & Guapan
Loyola
? gap
Andesite
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Fig. 3 Stratigraphical table, summarizing the molluscan evidence for the ages of the principal faunas discussed in this paper. It attempts to equate them with evidence from other sources (other macrofossils and microfossils, and radioactive dating of the andesite underlying the Loyola Formation of the Cuenca Basin). The principal molluscan faunas are also shown as being older than the Andean orogeny at the close of the Miocene. Note that the Mugrosa faunas of the Middle Magdalena Valley, Colombia, are shown as Lower Miocene, whilst rather indirect palynological evidence (Fig. 443, p. 323) suggests they might be Oligocene.

collection is much larger, consisting of well over a thousand specimens. It has been considerably enhanced in the course of the present study by the extraction of numerous small specimens from its rock matrix. It was made in about 1870, mainly from Pichana, but partly from Pebas itself, by a naturalist, Juan Hauxwell, who was said to have spent some thirty years exploring in the Amazon area. This collection was the subject of a paper by Woodward (1871) whilst Conrad, working in Philadelphia, was almost simultaneously (1871*a*, *b*) describing another large sample of Hauxwell's material. Most of the new species were described in Conrad's second paper: his nomenclature was followed by Woodward, who was clearly aware of Conrad's work.

In 1969 Parodiz reviewed the Tertiary non-marine faunas of South America: from the entire continent, a total of 137 species were dealt with. Parodiz never claimed that this work was comprehensive, and among several omissions are most of the brackish-water genera which occur in the Pebasian. More recently, Bristow & Parodiz (1982) have provided an account of the stratigraphy and a revision of the molluscan palaeontology of the Tertiary intermontane basins of Ecuador. Their material is divided between the Carnegie Museum, Pittsburgh and the BMNH (BMPD). Further revision herein shows that the faunal links suggested by Parodiz between these Ecuadorian faunas and those of the Pebasian are largely illusory.

The majority of the genera present in all these fossil faunas have living type species. The living South American freshwater molluscan fauna is, not surprisingly, comparatively unknown. The collections in the Zoology Department of the British Museum (Natural History) (BMZD) consist mainly of samples of type and figured specimens, dating from the nineteenth century. The general collection of comparative material is also somewhat inadequate, being both small and with, for the most part, imprecise locality data. In consequence, it has been difficult to investigate either variation within species or possible synonymies. Information on both the geographical ranges and habitats of species has had to be gleaned mostly from the literature, which is largely far from modern.

COLLECTIONS STUDIED AND ABBREVIATIONS

Collections studied

The list below gives the abbreviations used throughout the text for the institutions housing the collections studied.

ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.;

BMPD	Palaeontology Department, British Museum (Natural History);
BMZD	Zoology Department, British Museum (Natural History);
CAS	California Academy of Sciences, San Francisco, California, U.S.A.
NYSM	New York State Museum, Albany, New York State, U.S.A.;
PRI	Paleontological Research Institute, Ithaca, New York State, U.S.A.;
PIMUZ	Paläontologische Institut und Muzeum der Universität Zurich, CH-8006, Switzerland;
USNM	United States National Museum, Washington, DC, U.S.A.

Other material has been borrowed from: Naturhistorisches Museum, Basel, Switzerland; Muséum d'Histoire Naturelle, Genève, Switzerland; Zoologisches Staatsammlung, München, West Germany; and The Zoological Museum, University of Michigan, Ann Arbour, Michigan, U.S.A.

Abbreviations, etc.

The following abbreviations for dimensions are used:

br,	breadth
brap,	breadth of aperture
d,	diameter (instead of br for planorbiform gastropods)
diag,	diagonal
e,	estimated
h,	height
hap,	height of aperture
hbw,	height of body whorl
l,	length
lv,	left valve
rv,	right valve
sv,	single valve
vbr,	valve breadth (for single, disassociated valves of bivalves)
w,	width.

The spire angle (sa) of gastropods is measured across the periphery of the last whorl unless stated to the contrary.

Synonymies are constructed along the lines suggested by Matthews (1973). In all faunal lists, new taxa described therein are indicated by capital letters, and original material of other authors' which has been seen by me is indicated by 'v' Thus:

Pachydon OVALIS (sp. nov.)
v *PEBASIA dispar* (Conrad) (specimen seen) (gen. nov.)
v *LONGIVERENA EUCOSMIA* (Pilsbry & Olsson, 1935) (specimen seen) (gen. et. sp. nov.)

DESCRIPTIONS OF NEW LOCALITIES AND FAUNAS

La Tagua, Colombia (Eden and Weeda collections) 0° 05′ N, 74° 40′ W

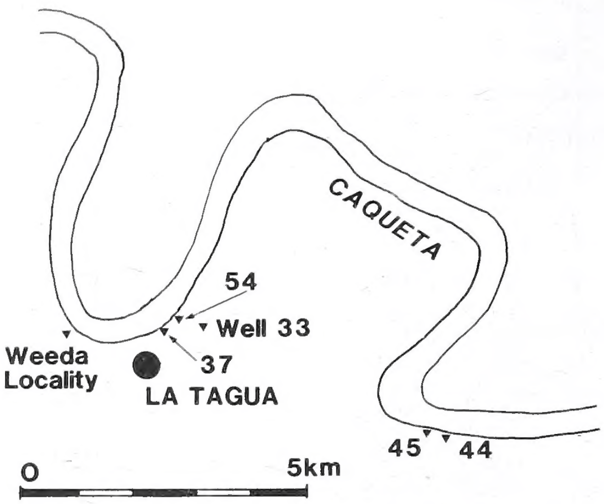


Fig. 4 La Tagua District. Map showing the relationships between the fossil localities in the La Tagua region, Colombia, based on a sketch map by M. J. Eden. Loc. 37 is at landing stage for La Tagua.

M. J. Eden and D. F. M. McGregor, both of Bedford College, London, and J. A. Morelo V of Istituto Geografico 'Agustin Codazzi', Bogotá, three geographers of the Colombian Amazonas Expedition (CAE), collected several samples of matrix rich in fossil molluscs from the La Tagua district of the Caqueta Valley, at *c*. 240 m above sea level (Eden, personal communication) during 1978, whilst primarily engaged in a geomorphological survey. Part of their work has appeared in Eden *et al*. (1982), in which a type section at Loc. CAE33 of the newly named La Tagua Beds was described (1982: 350–351). Nout Weeda, a Dutchman, then also working with CAE, independently discovered a different locality 1.5 km upstream from La Tagua. His material from this locality was passed to me in 1979 by Eden, at the same time as his collection from Puerto Nariño (p. 176). Unfortunately, there are no field notes with Weeda's collection, which has yielded many of the best-preserved fossils. However, it is fairly similar in both lithology and fauna to CAE33/570–670, but the rock is rather softer, so that the fossils are more easily extracted. Sheppard & Bate (1980) described a new ostracod fauna obtained from the only two La Tagua samples which they examined. That which they listed as CAE/GEO/33 was, in fact, from level 480–560 of the type section. The other was CAE/GEO/54. Details are given below; in many cases GEO is omitted for the sake of brevity.

My preliminary opinion that the La Tagua Beds might be correlated with the Pebas Beds of Brazil and Peru was quoted in Eden *et al*. (1982). Similar views were also quoted in Bristow & Parodiz (1982: 16, 19, 20). In the latter work my provisional identifications were given. Since then, I have studied both Weeda's collection and type material held in other museums, and a revised list of determinations is given below to avoid any further possible confusion.

determinations, Nuttall *in* Bristow & Parodiz (1982: 20)	**revised determinations**
Dyris gracilis	*Dyris* sp. indet.
Doryssa sp.	*Longiverena colombiana* sp. nov.
Cochliopina sp.	*Nanivitrea colombiana* sp. nov.
Aylacostoma browni	*Verena lataguensis* sp. nov.
Hydrobia cf. *ortoni*	*Dyris* sp. indet.
Anisothyris erectus	*Pachydon erectus* Conrad
Anisothyris sp.	*Pachydon hettneri* (Anderson)
unidentified unionids	*Diplodon (Ecuadorea)* aff. *bristowi* Parodiz and shell fragments

The only other known records of fossils from the region are those by Stirton (1953: 610), who stated that Axel Olsson and Donald Macgregor had found a possible caiman (Crocodilia) scapula in Tertiary clays and ferrugineous sandstone with *Unio* and other fresh-water fossils in the banks of Rio Guaybero five miles (8 km) below the mouth of Rio Heroru (*c.*1° 30′S, 73° 55′W). He also recorded a possible Oligocene *Eostoeiromys* sp. (Rodentia) from about 30 km east of La Tagua, at the confluence of Rio Peneyita and Rio Caqueta (*c.* 0° 07′S, 74° 22′W).

Type section of La Tagua Beds

Eden *et al.* (1982) designated the youngest Tertiary deposit of reddish surface sediments, often with a high silty component, as the Trinidad Bed. This shares the same type section as the La Tagua Beds in a recently dug water well, which is wide enough for a man to be lowered down with a rope to collect fossils and measure the section. This well is in La Tagua, 600 m from the river (Loc. CAE33). Here (1982: 351–352), 3.3 m thickness of Trinidad Bed overlies 3.4 m of La Tagua Beds exposed before the bottom of the well is reached. At other localities a much greater thickness of La Tagua Beds is reported, for instance over 14.2 m at CAE15 (1982: 354). The section at CAE33 is described fully in Eden *et al.* (1982); the following details are sufficient for this account.

Trinidad Bed	(0–330 cm)	
La Tagua Beds	(330–420 cm)	90 cm of light grey silty loam to silty clay, with yellowish brown to strong brown mottling. No fossils.
	(420–480 cm)	60 cm of light greyish brown to grey loam to sandy clay loam. Few fine unidentifiable shell fragments.
	(480–560 cm)	80 cm very dark grey shelly siltstone. Molluscs abundant, crowded together, mostly crushed.
	(560–570 cm)	10 cm described by Eden *et al.* as hardened lignite, with associated pyrites. It includes part of a fossilized branch, against which shells have drifted. Fossils abundant, mostly crushed, often partly pyritized.
	(570–670 cm)	100 cm light grey, rather hard siltstone. Fossils scattered throughout not arranged on bedding planes, and not as common as at two preceding horizons. Shells pale creamy coloured, shell material soft, easily damaged.
		[bottom of well]

CAE/GEO/33/480–560 cm

The sample of about 700 g (before processing) of partly carbonaceous grey clay, crowded with broken shell material most of which is fragmentary, yielded however some specimens good enough to identify and describe. The molluscs had to be extracted manually, using a needle sharpened to a chisel point, and needed hardening as development proceeded. Wetting the clay almost invariably resulted in the fossils disintegrating, and treatment with hydrogen peroxide, the method used to extract the ostracod fauna, proved useless for the molluscs. The following Mollusca were recovered:

Pachydon hettneri (Anderson)
Pachydon OVALIS sp. nov.
Pachydon erectus Conrad
Dyris tricarinata (Boettger)
Dyris SEMITUBERCULATA sp. nov.
Nanivitrea COLOMBIANA sp. nov.
Longiverena COLOMBIANA sp. nov.
Verena LATAGUENSIS sp. nov.

Eight of the eleven named fossil molluscan species known from La Tagua occur in this sample. The absentees are *Mytilopsis scripta* Conrad, from Sample 33/570–670, *Sheppardiconcha lataguensis* sp. nov. from Weeda's locality and CAE37, and *Diplodon (Ecuadorea)* aff. *bristowi* Parodiz from CAE54. In addition, unidentifiable *Dyris*, which do not belong to the two named species, occur in several samples. Shell fragments of naiades are also present. The age of the fauna is discussed at the end of the section. Extinct *Pachydon* may be indicative of brackish conditions whilst the living genera of Thiaridae, *Longiverena* and *Verena*, are river snails known only from fresh water. *Dyris*, which is common in the Pebasian, was presumably tolerant of brackish conditions. Living Littoridininae include the rather similar *Heleobia*, some species of which may be found in either fresh or brackish water (Marcus & Marcus 1963*a*, *b*, as *Littoridina*). This is the first fossil record of Cochliopinae, of which *Nanivitrea* is a member. The subfamily is generally freshwater, but its distribution, which includes the Pearl Islands off the Pacific coast of Panama and also islands of the Caribbean, suggests that some of its members have an ability to cope with salt water at some stage in their life cycle. All the species occur in profusion with the exception of *L. colombiana* and *V. lataguensis*. There are no traces of either pulmonate gastropods (fresh-water or terrestrial) or of the Corbiculacea, an almost exclusively fresh-water superfamily of bivalves, in any of the La Tagua samples. The naiades (Unionacea and Mutelacea) do occur elsewhere at La Tagua but not in sample 33/480–560.

Sheppard & Bate (1980) record the following ostracods:

(1) *Cytheridella POSTORNATA* Sheppard & Bate
(2) *Pelocypris zilchi* Triebel
(3) *Darwinula* sp.
(4) *Cypria AQUALICA* Sheppard & Bate
(5) *Perissocytheridea FORMOSA* Sheppard & Bate
(6) *RHADINOCYTHERURA AMAZONENSIS* Sheppard & Bate
(7) *Ambocythere CAMPANA* Sheppard & Bate
(8) *Cyprideis PURPERI COLOMBIAENSIS* Sheppard & Bate

The only other known occurrence of (1) is at La Tagua CAE54. Similarly, (2) is known only from its type occurrence in the ?Pleistocene of San Salvador. Species (3) to (7) were also described from the Pebasian, probably of Pichana (Woodward's sample of the Hauxwell Collection). *Cyprideis purperi purperi* Sheppard & Bate was described from the same Pichana sample and also occurs at CPCAN III, San Paulo da Olivença (Purper 1977) and at Canamá (herein, p. 328), both of which are Pebasian. Its subspecies *colombiaensis* is known only from 33/480–560.

Species (1) to (4) are indicative of fresh water, (5) and (8) of brackish conditions, whilst (6) and (7) belong to genera considered by Sheppard & Bate to be marine, *Rhadinocytherura* being newly described by them.

CAE/GEO/33/560–570 cm

This sample consisted of about 1 kg of shelly grey clay and carbonized wood. It appeared to be a shell drift which had accumulated against a tree-branch: part of the clay adjacent to the branch is pyritized. The fossils were even more difficult to extract and clean than those from the overlying level (480–560). The following molluscan fauna was recorded:

Pachydon hettneri (Anderson)
Pachydon OVALIS sp. nov.
Dyris sp. (or spp.) indet.
Longiverena cf. *COLOMBIANA* sp. nov.
Verena LATAGUENSIS sp. nov.

The fauna is very similar to that of the overlying sample (33/480–560): apparent absences of species are almost certainly because much of the fragmentary shell material was unidentifiable. The fauna could be indicative of brackish conditions, but fresh-water Thiaridae are also present.

CAE/GEO/33/570–670 cm

A sample of about 700 g of hard, pale grey, almost chalky marl, with fossils scattered randomly. Molluscan fauna:

Pachydon hettneri (Anderson)
Pachydon erectus Conrad
Mytilopsis scripta Conrad
Dyris sp. (or spp.) indet.
Longiverena cf. *COLOMBIANA* sp. nov.
(fragments only)

Only the rare and fragmentary *L. colombiana* is indicative of fresh water; all the other taxa are also tolerant of brackish water. The occurrence of rare specimens of *M. scripta*, resembling in its very triangular shape that figured by Pilsbry & Olsson (1935) from the La Cira fossil horizon of the Middle Magdalena Valley, is of particular interest.

CAE/GEO/37

From the southern (right) bank of Rio Caqueta, about 800 m downstream of La Tagua, the sample of about 350 g of dark, iron-stained, sandstone 'rotten-stone' is crowded with moulds of molluscs. Only three species can be recognized:

Pachydon hettneri (Anderson)
Pachydon OVALIS sp. nov.
Sheppardiconcha cf. *LATAGUENSIS* sp. nov.

Sheppardiconcha, an extinct genus of Thiaridae, probably lived in fresh water. *S. lataguensis* is better preserved at its type locality (1.5 km upstream from La Tagua; Weeda collection). *Pachydon*, indicative of brackish water, is very common at this locality. As in the other La Tagua samples, the brackish elements in the fauna dominate those of fresh water.

CAE/GEO/54

Immediately adjacent to, and downstream of, CAE37. The sample consisted of about 500 g of medium grey clay with bedding planes covered in shells, mainly small *Pachydon* with some *Dyris*. The other taxa are uncommon. Molluscan fauna:

Diplodon (Ecuadorea) aff. *bristowi* (Parodiz)
Pachydon hettneri (Anderson)
Pachydon erectus Conrad
Pachydon OVALIS sp. nov.
Dyris tricarinata (Boettger)
Dyris SEMITUBERCULATA sp. nov.
Nanivitrea COLOMBIANA sp. nov.
Longiverena COLOMBIANA sp. nov.

This is the type locality for the ostracod *Cythiridella postornata* Sheppard & Bate 1980, which also occurs in sample CAE33/480–560. It was described as a fresh-water species. The molluscs are the usual mixture of taxa with wide salinity tolerance accompanied by some of definite fresh-water origin. The single valve of the unionacean *D. (E.)* aff. *bristowi* is the only named naiad from La Tagua.

CAE/GEO/44

About 15 km downstream (6 km SE by E as the crow flies) from La Tagua, on right (south) bank of Rio Caqueta. Sample of 600 g of pale yellow to buff decalcified mudstone, with comparatively few, dark, rust-coloured moulds of shells scattered randomly throughout. It has been possible to make good latex casts showing sculptural details clearly from these moulds, which are not crowded together in an indeterminate mass as at CAE37. Only four species can be recognized:

Pachydon erectus Conrad
Pachydon hettneri (Anderson)
Pachydon cf. *OVALIS* sp. nov.
Longiverena COLOMBIANA sp. nov.

CAE/GEO/45

About 500 m upstream from CAE44. About 500 g of crumbly, dirty pale buff to grey limestone containing fossil shells with poorly preserved and extremely fragile surface sculpture. Fauna:

Pachydon erectus Conrad
Pachydon hettneri (Anderson)
Dyris cf. *SEMITUBERCULATA* sp. nov.
Nanivitrea cf. *COLOMBIANA* sp. nov.

A single turriculate shell which could be either *Sheppardiconcha* or *Longiverena* is also present. One specimen of each of the *Pachydon* species are well preserved.

Weeda Collection locality, 1.5 km upstream from La Tagua

About 300 g of pale grey, soft marl with fragile fossil shells which have well-preserved sculpture. Fossils were extracted by washing down the sediment with water. The process may be speeded up by the use of hydrogen peroxide. Fauna:

naiad shell fragments (probably Mutelacea)
Pachydon OVALIS sp. nov.
Dyris tricarinata (Boettger)
Dyris SEMITUBERCULATA sp. nov.
Nanivitrea COLOMBIANA sp. nov.
Sheppardiconcha LATAGUENSIS sp. nov.

This is the type locality of the four new species listed above. *Pachydon* is rare. This, in combination with the abundance of naiad shell fragments and the presence of *Sheppardiconcha*, suggests that the water at this locality might have been less brackish than usual during the deposition of the La Tagua Beds.

Age of the La Tagua Beds

The names of the eleven determinable molluscan species (six of which are new) of the La Tagua fauna are given above, pp. 173–4; the full ostracod fauna is also listed there. The ostracod fauna indicates a strong correlation between the La Tagua and the Pebas Beds. Sheppard & Bate (1980: 122, text-fig. 6) showed that of the 14 taxa (13 of which were new) in the combined fauna from the two regions, 8 occurred in the

La Tagua Beds, 11 in the Pebasian, 5 being common to both. In addition, different subspecies of *Cyprideis purperi* were found in the two regions. The only comparison that they make between these faunas and any other is their record of the probably Pleistocene species *Pelocypris zilchi* Triebel (1953) from San Salvador.

Diplodon (Ecuadorea) aff. *bristowi* Parodiz is the only naiad from the La Tagua Beds well enough preserved to be named. Parodiz' holotype (the only known specimen; see p. 273) is from the basal Loyola Formation of the Cuenca Basin.

Nanivitrea colombiana sp. nov. is the first fossil record of the genus from South America. Only one living species, *N. kugleri* (Forcart), which was described from Venezuela (as *Valvata*), is recognized from the continent.

No living species are known from the La Tagua fauna. The genera *Pachydon, Dyris* and *Sheppardiconcha* are extinct. None of the genera which are endemic (or almost so) to the Pebasian have been found at La Tagua: *Pebasia, Eubora, Toxosoma* and *Tropidobora* are all absent. It should be remembered that such a list is subject to alteration: until very recently it would have contained *Pachydon, Liris* and *Dyris* now all known to occur outside the Pebasian Basin, whilst *Pebasia* is described as new herein (p. 315). *Neritina* is important at many Pebasian localities but has not been found at La Tagua.

The La Cira fauna may represent a rather more fresh-water facies than that of La Tagua. Although *Pachydon* and *Mytilopsis* are present, the La Cira fauna contains four genera of naiades, *Triplodon* and *Diplodon (Rhipidodonta)* of the Unionacea and *Monocondylaea* and *Anodontites* of the Mutelacea, as well as the river snails *Verena* and *Longiverena.*

As shown above, the similarities between the La Tagua molluscan fauna and those of the inter-Andean basins of Ecuador are not particularly strong. Faunal lists in Bristow & Parodiz (1982) have been revised herein: see p. 172. They demonstrate that the Ecuadorean bivalve faunas are rich in fresh-water Unionacea, Mutelacea and Corbiculacea, whilst both *Pachydon* and *Mytilopsis* are lacking. In contrast, at La Tagua *Pachydon* and *Mytilopsis* are the only bivalves present except for *Diplodon (Ecuadorea)* aff. *bristowi* Parodiz and indeterminate naiad shell fragments. The Ecuadorian gastropod faunas are very different from those of La Tagua, being dominated by *Sheppardiconcha*. Both *Verena* and *Dyris* are present but uncommon. The presence of several other genera is more indicative of fresh than brackish water. Surprisingly, *Neritina*, though uncommon, occurs at several of the Ecuadorean localities. It is absent from La Tagua.

Sheppardiconcha, an extinct genus of Thiaridae perhaps most closely allied to *Basistoma*, was first described from the Cuenca Basin and also occurs in several Pebasian localities and at La Tagua (Weeda's locality only). *Verena lataguensis* has a rather aciculate spire and most resembles *V. browni* (Etheridge) which has a similar distribution to *Sheppardiconcha* in the Pebasian of the Amazon Basin. It also bears a strong resemblance to *V. barloventoensis* (Macsotay 1968), originally described as *Hemisinus*, from the Siquire Formation (?late Oligocene to early or middle Miocene) of Venezuela. A similar, high-spired, but unnamed *Verena* occurs in the Cuenca Basin. The species of *Verena* known from the Magdalena Valley Tertiary *(Hemisinus avus* and *H. laevicarina*, both of Pilsbry & Olsson, and *Ampullaria guaduasensis* (Anderson)) have low obtuse spires like the living type species, *V. crenocarina* (Moricand), and do not resemble *V. lataguensis* closely.

Dyris is represented by several fairly common species in the Pebasian, from which it was described, but its only known representative in the Magdalena Basin is the poorly preserved *D. lacirana* (Pilsbry & Olsson). At La Tagua it is an important element of the fauna, as both named species and numerous specifically indeterminate specimens, possibly representing more than one species. *D. tricarinata* (Boettger) is apparently a highly variable species. Perhaps more than one species is grouped under this name: already the rather similar *D. hauxwelli* sp. nov. has been separated from this 'group', and in the circumstances it would seem unwise to claim a close correlation between the Pebasian, the La Tagua Beds and also the San Cayetano Formation of the Loja Basin, Ecuador on the basis that all three contain *D. tricarinata. D. semituberculata* sp. nov. is easily distinguished from the other described species of the genus by its collabral wrinkling. Its variable spiral sculpture is reminiscent of that found in two Pebasian species, *D. lintea* (Conrad) and *D. tricarinata*.

The La Tagua specimens (CAE33/570–670) identified herein as *Pachydon erectus* have some resemblance to its subspecies *elongatus* (Boettger) from the Pebasian; *P. erectus* (s.s.) Conrad, also Pebasian, is in contrast the largest known species of *Pachydon. P. ovalis* sp. nov. has some resemblance to *P. amazonensis* from the Pebasian.

The molluscan fauna of the La Tagua Beds provides links between the Pebasian of the Amazon Basin and the non-marine Tertiary of the Magdalena Valley, lying to the west of the Eastern Cordillera. It also shows a slight resemblance to the several faunas of the inter-Andean Tertiary basins of Ecuador.

Pachydon hettneri was first described by Anderson (1928) from near San Juan de Rio Seco in the Upper Magdalena Valley. This species is very distinctive because of its strong posterior diagonal angulation and prominent corselet. It was the dominant member, occurring in great profusion, of a small brackish-water fauna which he thought came from the Eocene Guaduas Series. This fauna, which is now referred to the Santa Teresa Formation, is discussed herein (p. 335) and is now thought to be, at the earliest, late Oligocene, but is almost certainly Miocene. At La Tagua, this species is among the most common, occurring in the majority of samples.

Longiverena colombiana, although described herein as a new species, is nevertheless very similar to *L. eucosmia* (Pilsbry & Olsson 1935) which was described from the Mugrosa fossil horizon of the Middle Magdalena Valley. It is now thought that several other nominal species these authors described, both from this horizon and from the overlying La Cira fossil horizon of probable Miocene age, are referable to this species. In addition, both *Semisinus peyeri* de Greve, from the Pebasian of Iquitos, and its subspecies *dickersoni* Palmer, from the Loyola formation of the Cuenca basin, Ecuador, are here regarded as synonyms of *L. eucosmia*. It may be suggested that there is no great difference in the ages of all the deposits in which this species and the similar *L. colombiana* have been found. This, too, points to a Miocene age.

Specimens of the Pebasian species *Mytilopsis scripta* Conrad, with very triangular shells and characterized by straight hinge lines and markedly angular diagonal umbonal ridges, occur at CAE33/570–670. They are very similar to those described from Canamá on Rio Javari as *M. acuta* (Etheridge) and from the La Cira horizon as *M. cira* (Pilsbry & Olsson 1935). *Mytilopsis* is byssally attached, and if, as frequently happens, individuals grow crowded together, they may show wide variation in shape. The other species of *Mytilopsis* occurring in the Pebasian (but not found at either La Tagua or La Cira) is the living *M. sallei* (Recluz), which is characterized by a curved hinge line. As *M. sallei* is now recognized as occurring in the late Oligocene, it is clear that no precise stratigraphical conclusions should be based on occurrences of this genus.

The above analysis establishes that the facies in these different basins are not strictly comparable. It is difficult to pursue this point much further because it is known that many of the other faunas under consideration are 'mixed' in the sense that they come from more than one locality, and the accurate data necessary to disentangle them is not always available. If it is accepted that the La Tagua facies is not exactly similar to that pertaining in any of the other basins, then it must follow that the generic composition of the faunas is not necessarily going to be identical. The greater the number of genera in common, the greater the possible number of species in common: the converse is obviously true.

In these circumstances the presence of *Pachydon hettneri* (Anderson), *Mytilopsis scripta* Conrad and *Longiverena colombiana* sp. nov. in the La Tagua fauna suggests that its age may well be similar to that of the *Pachydon hettneri* horizon (Santa Teresa Formation) of the Upper Magdalena Valley and to its supposed correlative, the La Cira fauna of the Middle Magdalena Valley. At the same time, the presence of *Pachydon erectus* Conrad and *Dyris tricarinata* (Boettger) suggests that the La Tagua fauna is of more or less similar age to the Pebasian, which being the only one to contain living species is likely to be younger than the other fossil faunas under consideration.

An age within the Miocene is therefore favoured for the La Tagua fauna.

Puerto Nariño, Colombia (Weeda collection) 3° 38′ S, 70° 33′ W

Puerto Nariño lies some 60 km west of Leticia on the northern (left, Colombian) side of Rio Solimões, at about the above position. It is reasonably close to two classic Pebasian localities, Canamá (Etheridge 1879) and Três Unidos (Roxo 1924), both of which lie to the south, on Rio Javari. The collection was made by Mr Nout Weeda, and was handed to me for study, along with his collection from La Tagua, by M. J. Eden in 1979. No further details about the locality are known.

The single sample consisted of about 700 g of friable, rather silty, pale grey to dark grey, carbonaceous clay, which had disintegarated into small lumps about 15 mm in diameter. The sample contains well over a thousand fossil shells, many of which were already virtually free of matrix. Almost undamaged shells and badly broken specimens are about equally common. Bivalves with the two valves together are extremely rare. Further cleaning of half the sample was accomplished by treating it with dilute hydrogen peroxide. The residue is dominated by *Verena browni* (Etheridge) and *Liris scalarioides* (Etheridge), and to a lesser extent by *Toxosoma eborea* Conrad and the two species of *Dyris* present. Only three species of *Pachydon* have been found here: *P. trigonalis* sp. nov. is reasonably common, but both *P. cuneatus* Conrad and *P. tenuis* Gabb are rare. All the *Ostomya* specimens consist only of broken pieces showing the hinge characters of the genus. Both *Pebasia* and *Mytilopsis* are represented by one valve each. Nacreous shell fragments of naiades – usually about 10 mm across – are extremely common. Their prismatic layer, on which the sculpture occurs, has invariably been worn away, so that it is not possible to assign them even to their correct superfamily. One gastropod shell fragment, about 3 cm across, is identified as *Ampullaria*. The following Mollusca are recorded:

Pachydon tenuis Gabb
Pachydon cuneatus Conrad
Pachydon TRIGONALIS sp. nov.
Pebasia dispar (Conrad)
Ostomya sp. indet.
Mytilopsis sallei (Recluz)
Dyris ortoni (Conrad)
Dyris lintea (Conrad)
Liris scalarioides (Etheridge)
Toxosoma eborea Conrad
Verena browni (Etheridge)
Ampullaria (s.l.) sp. indet.

Although undoubtedly Pebasian, this fauna differs from those of the classic faunas of Pichana and Iquitos in several ways. It is highly fossiliferous, yet only twelve taxa have been found. However, it is not known whether the fossils came from only one level or whether several different layers were sampled; it is thus idle to speculate on how complete the collection is. The present fauna contains only three species of *Pachydon*, instead of the seven or eight which might be expected. Moreover, *P. trigonalis* is new, though also known to occur at Canamá, having been extracted from matrix in the course of the present study. The Puerto Nariño shells of one of the other species, *P. cuneatus*, are slightly atypical. It is one of the rarest at Iquitos and Pichana: at both these localities the most common species of *Pachydon* are *P. tenuis* Gabb, *P. erectus* Conrad, and the type species *P. obliquus* Gabb. Both *Ostomya* and *Mytilopsis* are always uncommon, if present. The specimens assigned to both of the *Dyris* species listed above appear to be slightly unusual and perhaps local variants. Other species of *Dyris*, including the normally common *D. tricarinata* (Boettger), are absent.

Liris scalarioides appears from de Greve's illustrations (1938), misidentified as *Liris minuscula* (Gabb), to be common at Iquitos. It was orginally described from Canamá. Its full geographical distribution is not known: its presence at other localities under different specific names can only be assessed when good figures are available. The Puerto Nariño specimens assigned to *Toxosoma eborea* are also slightly atypical of the species, being rather larger and having a more rounded profile to the body whorl than is usual in specimens from Pichana and Canamá. It is the only species of the genus, which is endemic to the Pebasian. The specimens identified as *Verena browni* (Etheridge) are certainly conspecific with shells wrongly determined as *Aylacostoma sulcata* (Conrad) from Três Unidos (Parodiz 1969), as Parodiz himself acknowledged (personal communication). They are also similar to Etheridge's type illustration of the species from Canamá, but some slight doubt must remain about this determination as the type material is lost. Notable absentees from the Puerto Nariño fauna include *Eubora* and *Tropidobora*, both endemic to the Pebasian, and *Neritina*, which is common in most Pebasian faunas including Pichana, Iquitos, Canamá and Três Unidos.

The presence – assuming correct identification – of *Verena browni* also at Canamá and Três Unidos and the occurrence of *Pachydon trigonalis* at Canamá suggests that these two faunas are more similar than others to the Puerto Nariño

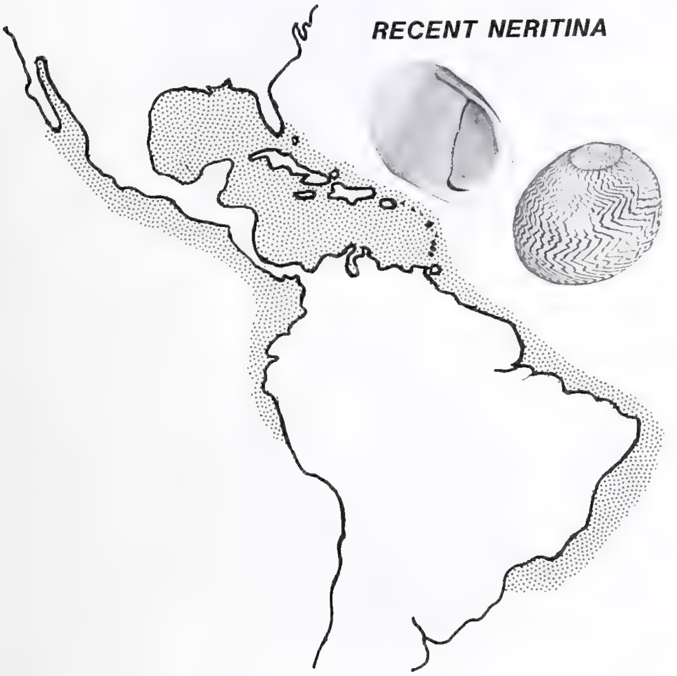


Fig. 5 Recent distribution of *Neritina*. Insets: top, front view of *N. lineolata* (Lamarck), Para, Brazil; bottom, rear view of *N. zebra* (Bruguière), Surinam; both about × 1.

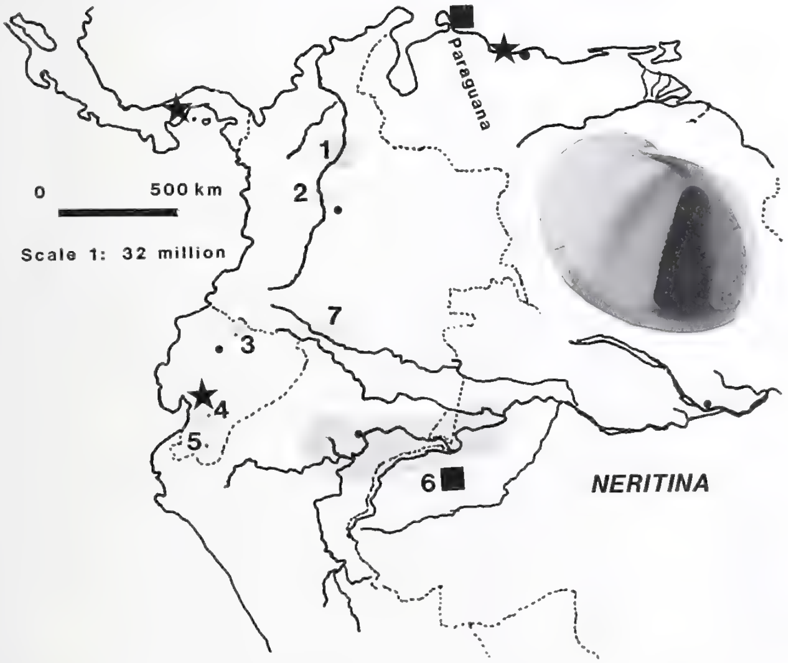
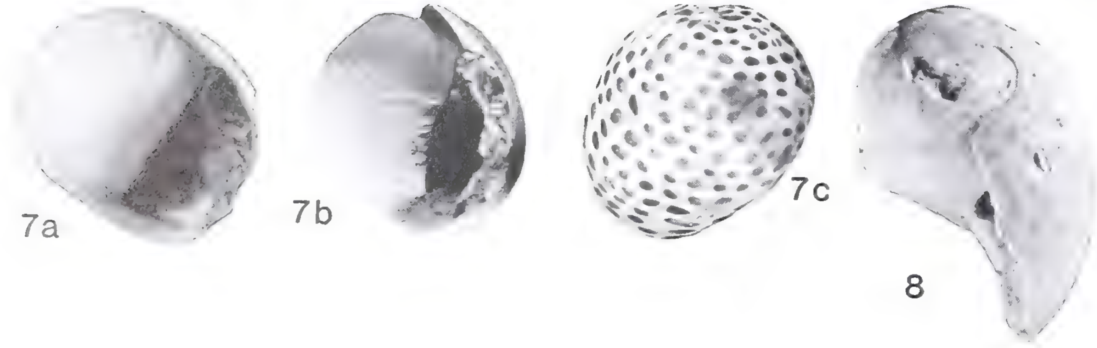


Fig. 6 Neogene distribution of *Neritina*. ■ = *N. ortoni* Conrad; ★ = other species. The genus is uncommon during the Neogene in the Caribbean region but has been recorded from Jamaica and the Dominican Republic.
Key: 1, Middle Magdalena deposits (Pilsbry & Olsson 1935); 2, Upper Magdalena Valley (Anderson 1928, Butler 1942, Porta 1966); 3, Chota Basin, 4, Cuenca Basin and 5, Loja and Malacatos Basins (all Bristow & Parodiz 1982); 6, Pebasian Basin (numerous authors and herein); 7, La Tagua (herein).

fauna. These three geographically close localities appear to form a natural group within the Pebasian. It should be pointed out, however, that the sediments of Puerto Nariño and Canamá preserved in BMPD are very different.

The Puerto Nariño fauna may represent a rather less brackish facies than is usual in the Pebasian, but the positive evidence for this is not great. *V. browni* is the only member of the fresh-water Thiaridae present, but it is extremely common. *Ostomya, Dyris, Liris* and *Toxosoma* are typical of the Pebasian and therefore are assumed to tolerate brackish conditions. The negative evidence consists of the comparative rarity of *Pachydon*, the great rarity of *Mytilopsis* and the absence of *Neritina*. In addition, naiad shell fragments are extremely abundant and certainly much more common than in the single Hauxwell Collection concretion from Pichana. This suggests that some fresh-water habitat existed not far away.



Figs 7–8 *Neritina ortoni* Conrad. Pebasian, Canamá, Peru; Brown Colln. **7a-c**, GG19993, **lectotype** (herein selected) of *Neritina puncta* Etheridge, 1879; front view, oblique view into aperture, rear view. **8**, GG21777, a paralectotype of the same, showing apical region. All × 5.

SYSTEMATIC PALAEONTOLOGY

Class **GASTROPODA** Cuvier
Subclass **PROSOBRANCHIA** Milne Edwards
Order **ARCHAEOGASTROPODA** Thiele

Superfamily **NERITACEA** Lamarck, 1809

[*nom. transl*. Thiele (1929: 71), *ex* neritacées Lamarck (1809: 319); Neritacea Rafinesque (1815: 144) (family); Neritadae Fleming (1828: 318) (family)].

Family **NERITIDAE** Lamarck, 1809

[*nom. correct*. Gray (1840: 147)]

Subfamily **NERITINAE** Lamarck, 1809

[*nom. transl*. Swainson (1840: 239, 346)]

Neritacea and Neritidae are here attributed to Lamarck (1809). This predates the usually accepted authorship of Rafinesque (1815) quoted by Keen *in* Moore (1960: I275).

Genus ? ***NERITINA*** Lamarck, 1816

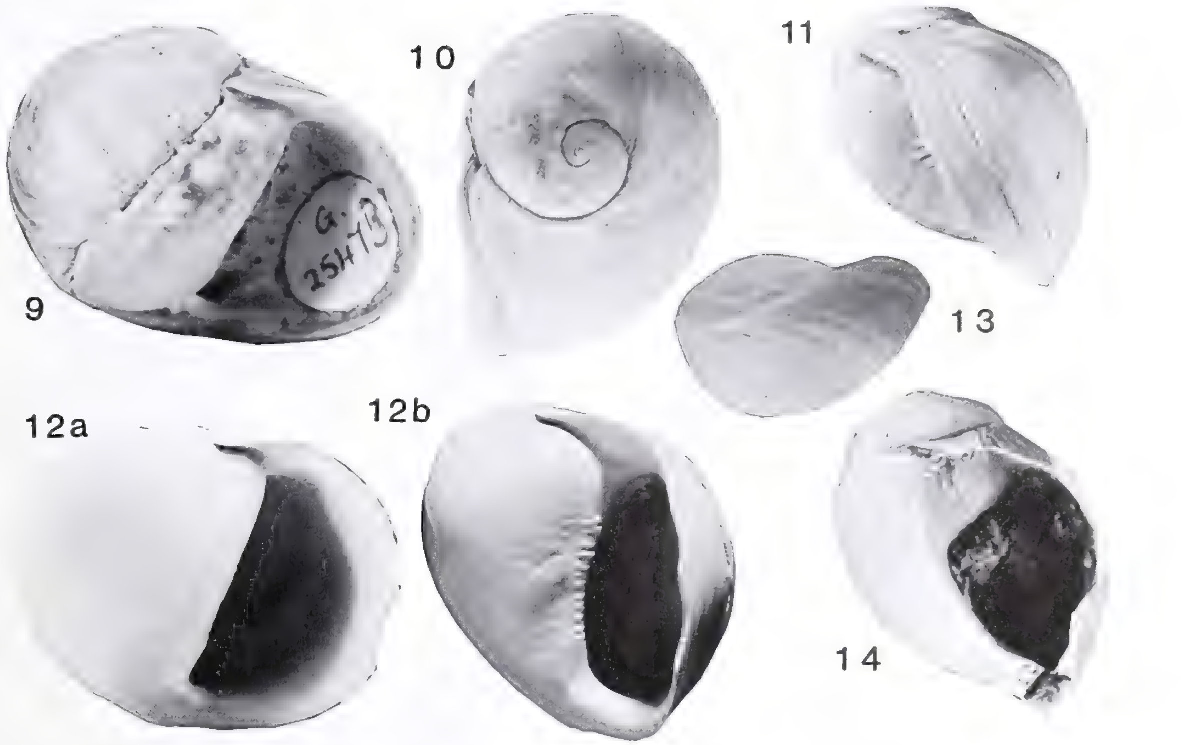
TYPE SPECIES. *Nerita pulligera* Linné, 1766 (ICZN Opinion 119, 1931). Recent, Indo-Pacific.

REMARKS. The Pebasian Neritininae are here all placed within one species, *Neritina ortoni* Conrad, 1871. This is close to, and possibly conspecific with, a shell from the Miocene of Venezuela identified by Jung (1965) as *Neritina* aff. *woodwardi* Guppy (1866) originally described from the Neogene of Jamaica.

Some doubt must be expressed about the generic assignment of *ortoni*. Firstly, it has been impossible to find any other reasonably similar species, either fossil or Recent, from either the western Pacific or the Caribbean (Flores & Cáceras 1973, Keen 1971, Russell 1941). Secondly, the apertural features are reminiscent of, but by no means identical to, two marine genera with extremely widespread distribution: the large patelliform *Velates* (Cretaceous–Eocene) and the much smaller (*c*. 5 mm diameter) *Smaragdia* (Neogene–Recent), which is placed in its own Subfamily Smaragdiinae. Thirdly, the only operculum extracted from the matrix from Pichana, although broken, cannot be matched with that of either *Neritina*, *Theodoxus* or *Smaragdia*. The operculum of *Velates* has not been seen. In the present specimen, the peg which branches off the apophysis is missing, and this appears to be an original feature rather than as a result of damage to the specimen. The operculum of *Fluvinerita* (Recent, Jamaica) also lacks the peg, but the shell is different, and the genus seems to have been correctly placed by its original author (Pilsbry 1932) as a subgenus of *Nerita*. The operculum of *Smaragdia*, although similar to that of *N. ortoni* in general shape, does have a peg. These points are discussed below in further detail.

? Neritina ortoni Conrad, 1871 Figs 7–28

. 1869 *Neritina pupa* (Linné); Gabb: 197; pl. 16, fig. 2.
*. 1871*b* *Neritina ortoni* Conrad: 195; pl. 10, figs 5, 11.
v. 1871 *Neritina ortoni* Conrad; Woodward: 103; pl. 5, figs 2a, b.
. 1878 *Neritina ortoni* Conrad; Boettger: 428.
v. 1879 *Neritina ziczac* Etheridge: 85; pl. 7, figs 10, 10a.
v. 1879 *Neritina puncta* Etheridge: 85; pl. 7, fig. 9.
. 1906 *Neritina ortoni* Conrad; Clarke: 132.
. 1924 *Neritina ortoni* Conrad; Roxo: 47.
. 1924 *Neritina puncta* Etheridge; Roxo: 47.
. 1924 *Neritina etheridgei* Roxo: 47, nom. nov. pro *Neritina ziczac* Etheridge, 1879 non *Neritina zigzag* Lamarck, 1822: 185.
. 1924 *Neritina*, unnamed species; Roxo: figs B, B′.
. 1938 *Neritina (Vitta) ortoni* Conrad; de Greve: 61; pl. 5, figs 12–15.
v. 1938 *Neritina amazonensis* de Greve: 62; pl. 5, figs 4–6, 8.
v. 1938 *Neritina roxoi* de Greve: 64; pl. 5, figs 10, 11, 16.
. 1938 *Neritina (Vitta) etheridgei* Roxo; de Greve: 66; pl. 5, figs 1–3, 7, 9.
. 1938 *Neritina puncta* Etheridge; de Greve: 67 (discussed but not recorded as being present at Iquitos).
v? 1965 *Neritina* aff. *woodwardi* Guppy; Jung: 480; pl. 62, figs 12, 13.
. 1966 *Neritina amazonensis* de Greve; Willard: 66; pl. 62, fig. 3.



Figs 9–14 *Neritina ortoni* Conrad. Pebasian, Pichana, Peru; Hauxwell Colln. **9**, GG25473, shell figured by Woodward (1871: pl. 5, figs 2a, b), tilted front view × 2. **10**, GG25474, shell accompanying GG25473, top × 2. **11**, GG21783, side, showing sinuate outer lip, × 2.5. **12**a, b, GG21782, front, oblique view into aperture to show columella, × 2.5. **13**, GG21784, base × 2. **14**, GG21785, similar view to Fig. 11, but with outer lip broken away showing columella, × 2.5.

. 1966 *Neritina etheridgei* Roxo; Willard: 66, 67; pl. 62, figs 1, 2.
. 1966 *Neritina ortoni* Conrad; Willard: 66.
. 1966 *Neritina puncta* Etheridge; Willard: 66.

TYPE MATERIAL. Types of *N. ortoni* Conrad, 1871, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Collection) (NYSM, Clarke 1906). Not studied.

Lectotype of *N. puncta* Etheridge, 1879, selected herein. BMPD GG19992, Late Caenozoic, Pebasian, Canamá, Peru (Barrington Brown Collection); probably the specimen figured by Etheridge, pl. 7, fig. 9. Two accompanying, probably unfigured, shells, GG19993, GG21777, details as above, are paralectotypes.

Lectotype of *N. ziczac* Etheridge, 1879, selected herein. BMPD GG19994, Late Caenozoic, Pebasian, Canamá, Peru (Barrington Brown Collection); the original of his pl. 7, fig. 10 (front view). GG19995, details as above, figured by Etheridge, pl. 7, fig. 10a (rear view), is a paralectotype.

Holotype of *N. amazonensis* de Greve, 1938: pl. 5, figs 4, 5, 6, 8. PIMUZ 219, Late Caenozoic, Iquitos, Peru (Peyer Collection). ('Typus' of de Greve). PIMUZ 220, details as above, but not figured by de Greve, is a paratype.

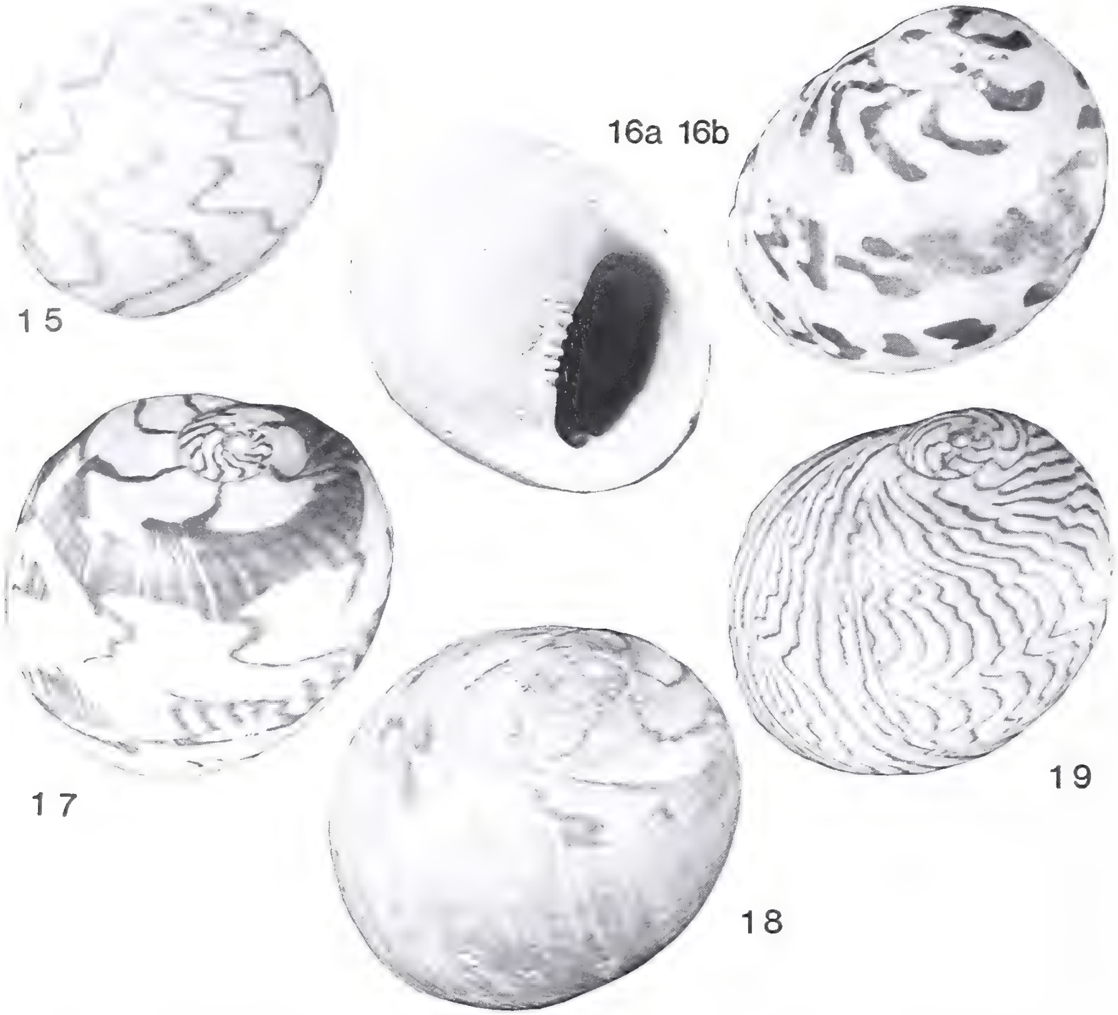
Holotype of *N. roxoi* de Greve, 1938: pl. 5, figs 11, 16. PIMUZ 216B, Iquitos, details as for *N. amazonensis*. Another shell figured by de Greve, pl. 5, fig. 10, is a paratype; these two are accompanied by a third unnumbered shell which was not mentioned by de Greve and is therefore not a paratype.

OTHER MATERIAL STUDIED. G25473, Late Caenozoic, Pebasian, Pichana, Peru (Hauxwell Colln), the shell figured by Woodward, 1871: pl. 5, figs 2a, b, and G25474, the accompanying shell. G24587/1–30, GG19997/1–20, GG21782–99, Pichana, same details. GG19996, a single operculum, extracted in 1982 from matrix of Hauxwell Colln from Pichana. GG12282/1–12, GG12283/1–25, GG21778–81, Late Cainozoic, Amazon Valley (Trechmann Colln). H 13639 (Basel NHM), Cantaure Formation, Late Burdigalian, Lower Miocene; Paraguana Peninsula, northern Venezuela (Jung 1965); see Fig. 25.

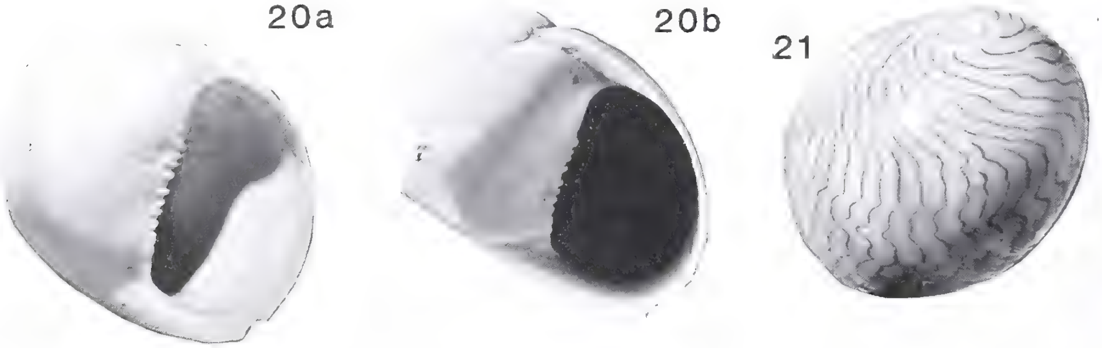
FURTHER OCCURRENCES. All late Caenozoic, Pebasian. Pebas (Gabb 1869, Boettger 1878, Willard 1966); Três Unidos, Peru (Roxo 1924); Iquitos (de Greve 1938, Willard 1966); Negro Urca and Rumi Tuni (Willard 1966). Late Caenozoic, Pebasian, upper Amazon Valley and ? Lower Miocene, northern Venezuela.

DIAGNOSIS. *Neritina* characterized by markedly angular, velatiform, junction between inner lip callus and basal ridge of shell; upper surface of shell varying between domed with sunken nuclear whorls to almost flat with exserted nuclear whorls; outer lip flared, with sinuous growth lines; inner lip denticulate except at upper and lower ends; colour patterning variable, commonly of zigzag lines but sometimes of variously shaped blotches and irregular reticulations; operculum lacking peg.

DESCRIPTION. The shell surface is smooth and porcellanous, but the growth lines are clearly visible. There are seldom more than four whorls. The spire varies: in most specimens it is almost flat except for the small, globular, first whorl which stands proud of the main shell surface. In these shells the suture describes a smooth spiral. In a relatively few other shells, the spire is domed, or papilliform, but the nuclear

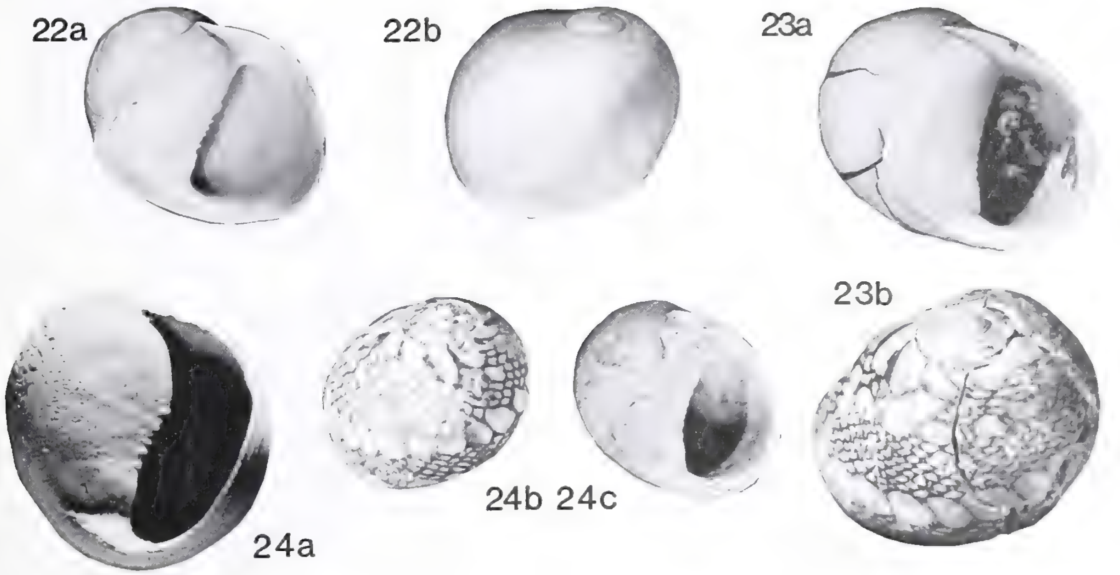


Figs 15–19 *Neritina ortoni* Conrad. Pebasian, Pichana, Peru; Hauxwell Colln. **15**, GG21789, rear × 10. **16**a, b, GG21786, front and rear, × 6.7. **17**, GG21787, rear × 5. **18**, GG21790, rear × 3. **19**, GG21788, rear, showing most common form of colour patterning, × 5.



Figs 20–21 *Neritina ortoni* Conrad. Pebasian, Canamá, Peru. **20**a, b, two apertural views from different angles of GG19994, **lectotype** (selected herein) of *Neritina ziczac* Etheridge, figured by Etheridge (1879: pl. 7, fig. 10), × 2.5. **21**, rear view of GG19995, showing colour patterning, × 2.5.

whorl is sunken or almost so, and their suture describes a rather erratic spiral with angular changes of direction. In all shells the expansion rate is high, producing a flared outer lip, which, in side view, is markedly sinuous. Both the upper and lower junctions between the outer lip and the main body of the shell are reminiscent of *Velates*. As in *Velates*, an angular basal ridge starts at the left lower edge of the callus pad and runs parallel to the base of the shell along the lower margin of the inner lip. The outer lip is thickened at its upper junction with the inner lip. The inner lip appears straight when viewed from the front, but is curved to the right in side view. The number of denticles borne by the inner lip varies considerably, but only partly with shell size: between ten and sixteen denticles may be present on fully grown shells. The denticles



Figs 22–24 *Neritina ortoni* Conrad. Pebasian, Iquitos, Peru; Peyer Colln (PIMUZ). **22**a, b, PIMUZ 219, holotype of *Neritina amazonensis* de Greve, front and rear, × 2. **23**a, b, PIMUZ 216A, paratype of *Neritina roxoi* de Greve, front and rear, × 4. **24**a–c, PIMUZ 216D, holotype of *Neritina roxoi* de Greve, front and rear, × 4, oblique view into aperture, × 6.

are absent from both the top and bottom of the inner lip. The callus pad covers a large proportion of the apertural surface, upon which it has a slight flattening effect.

Colour patterning is visible on the majority of shells, but there is a strong tendency for the patterning to break down on the last whorl of the larger specimens. The most common pattern is of zigzag lines. Patterns of both regular and irregular dark blotches are present in a minority of specimens. A reversal of this also occurs: in some shells light blotches are separated by a dark, rather irregular, net-like pattern.

A single damaged operculum was obtained from the matrix from Pichana. It lacks the peg which branches off the apophysis in other species of *Neritina*.

Dimensions. In mm.	height	breadth
Conrad 1871: pl. 10, fig. 5.	17	17
Conrad 1871: pl. 10, fig. 11.	24	26
G25473 (fig'd Woodward 1871: pl. 5, figs 2a, b)	22.3	24.0
G25474 (found with G25473)	23.5	24.2
GG19992, lectotype, *N. puncta* Etheridge, Canamá	7.5	7.5
GG19993, paralectotype, *N. puncta* Etheridge, Canamá	6.4	6.4
GG21777, as above.	8.4	–
GG19994, lectotype, *N. ziczac* Etheridge, Canamá.	16.5	16.5
PIMUZ 219, holotype of *N. amazonensis* de Greve, Iquitos.	14.2	16.0
PIMUZ 216A, holotype of *N. roxoi* de Greve, Iquitos	8.4	8.4
H 13639 (Basel NHM), fig'd Jung, 1965 as *N.* aff. *woodwardi* Guppy; Cantaure Formation, Venezuela.	13.5	15.0

Remarks. Conrad (1871) remarked that Gabb (1869) had only young shells, which were identified as *N. pupa* Linné, available for study. Conrad, who had fifteen shells of various ages, concluded that both his own and Gabb's material belonged to a single new species, *N. ortoni*. The living *N. pupa* was much smaller and its spire was not flattened.

The BMPD collections, including specimens newly extracted from matrix, contains about 100 shells from Pichana, far fewer than the over 250 quoted by Woodward (1871). Nevertheless, his conclusion that *N. ortoni* is the only *Neritina* occurring there is still supported. Spire shape appears to be a very variable feature, and Woodward's conclusion, based only on his Pichana sample, that only one species is present, is now expanded to cover all the references in the above synonymy. The sample from Pichana is predominantly of shells with zigzag colour patterning, though other patterns occur. The unlocalized samples (GG12282–3, Trechmann Colln) also have a preponderance of zigzag colour-patterned shells, but show marked variation in spire height, with about a third of the undamaged shells having the relatively high, domed, spire coupled with a sunken nucleus. In shape, these agree with the much smaller lectotype and two paralectotypes of *N. puncta* Etheridge, 1879, from Canamá. *N. ziczac* Etheridge, 1879, also from Canamá, and subsequently renamed as *N. etheridgei* by Roxo (1924), has the typical zigzag patterning of *N. ortoni*: there appear to be no differences between the two species, and it is difficult to understand why Etheridge described his material under a new name. De Greve (1938) used the name *N. etheridgei* Roxo for adults with zigzag markings and *N. ortoni* for juvenile shells up to 4.3 mm high with similar patterning. His *N. amazonensis* was based on large shells with little or no patterning, but such obsolescence is a regular feature of the larger shells at Pichana. *N. roxoi* de Greve was erected for shells from Iquitos resembling the unnamed specimen from Três Unidos figured by Roxo (1924: figs B, B′). These have domed spires and an irregular, diagonally reticulate pattern modified by larger clear oval patches arranged spirally. Somewhat similar patterning occurs rarely at Pichana (BMPD and Conrad, 1871*b*: pl. 10, fig. 5). This patterning appears to form a link between the zigzag lines of typical *N. ortoni* and the dark

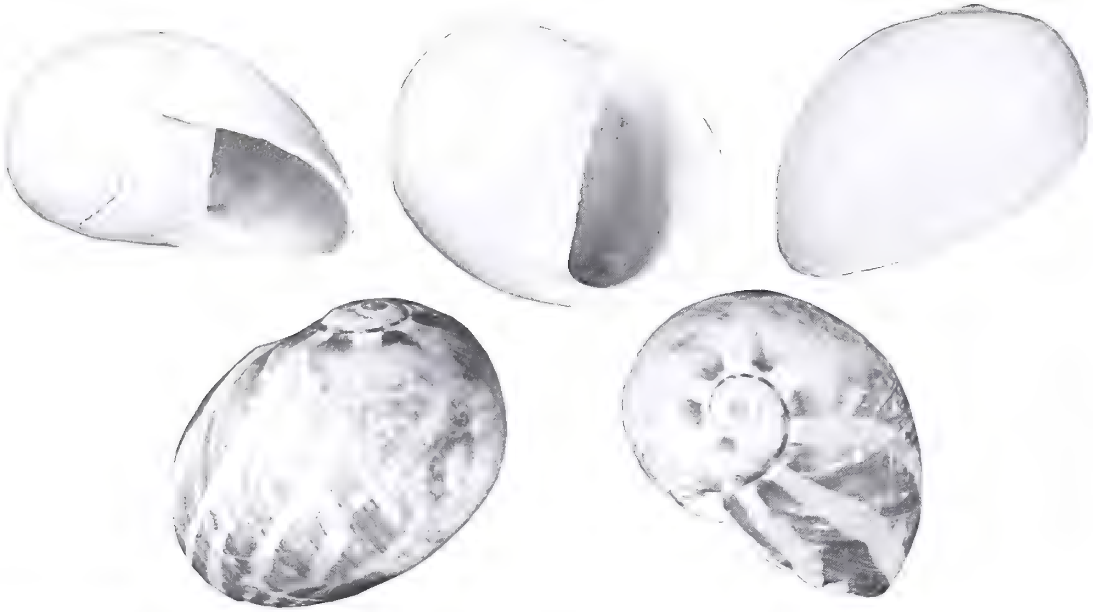
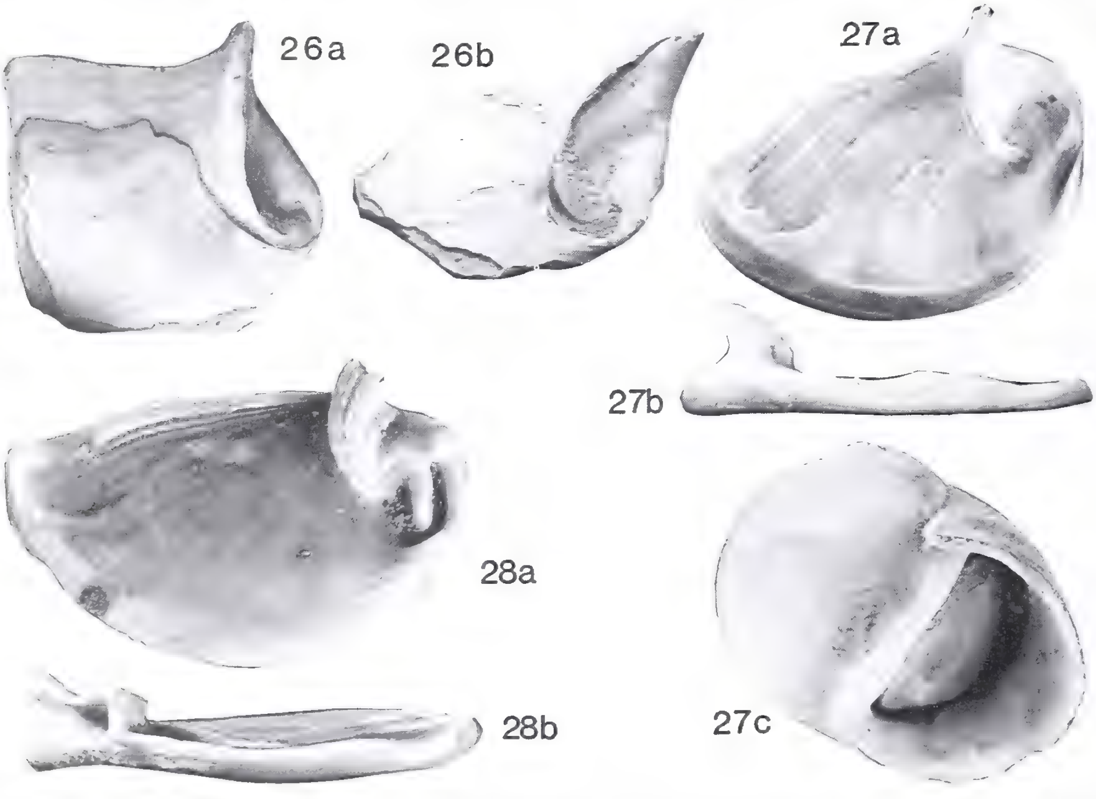


Fig. 25 *Neritina ?ortoni* Conrad. Lower Miocene, Late Burdigalian (planktonic foraminiferal zone N.8), Cantaure Formation, Paraguana Peninsula, northern Venezuela. Basel NHM, H 13639, figured Jung (1965: pl. 62, figs 12, 13) as *N.* aff. *woodwardi* Guppy, all × 2.5.



Figs 26–28 Operculae. **26**a, b, GG19996, broken operculum, presumed to be of *Neritina ortoni* Conrad, extracted from washings from Pebasian, Pichana, Peru, Hauxwell Colln. Plan and oblique views, × 10. **27**a–c, *Fluvinerita tenebricosa* C. B. Adams. ANSP 15359, paratype of *Nerita (Fluvinerita) alticolor* Pilsbry; Recent, Jamaica. **27**a, b, plan and side views of operculum × 8; **27**c, shell × 5. **28**a, b, *Neritina reclivita* Say. BMZD 1984223, Recent, Caribbean; plan and side views of operculum × 4.

spots which tend to coalesce into broad radiating spokes on the spire of *N. puncta*.

The most striking feature common to all the nominal species of Pebasian *Neritina* is the shallowness of the insertion of the inner lip within the aperture, particularly abapically where the basal ridge and the inner lip are almost flush with each other. These apertural features are reminiscent of those found in *Velates*, *Smaragdia*, and the shell identified as *N.* aff. *woodwardi* Guppy by Jung (1965), but are unknown in other Neritinae. However, the Eocene marine genus *Velates* may be distinguished by its characteristic patelliform aboral surface. *Smaragdia* differs in the way in which the central part of its inner lip is stepped to the left and by its small size. Its rather curved growth lines, however, resemble those of *N. ortoni*.

Examination of living species of *Neritina* from both the Pacific and Atlantic/Caribbean shores of South and Central America has revealed none particularly close to *N. ortoni*: in addition to lacking the velatiform aperture, they have operculae with pegs. *N. zebra* (Bruguière, 1792*a*) often has zigzag patterning, but the individual lines are more continuous, with fewer angulations, and generally broader. More important differences are its more evenly globose shape and its virtually straight outer lip. *N. zebra* appears to be confined to the Atlantic drainage system from Panama to north-western Brazil (von Martens 1879: 118, who added that, as far as is known, it lives in fresh running water). However, von Martens recorded it from the island of Curaçao, so it must clearly be able to tolerate some contact with salt water.

Nerita (Fluvinerita) alticolor Pilsbry (1932) [= *Neritina tenebricosa* C. B. Adams, 1852] lives in fresh-water streams of Jamaica and has an operculum which differs in detail from that of *N. ortoni* but does lack a peg. The shell, however, is relatively thick and also spirally striate. It is rather globose as well as lacking the apertural features of *N. ortoni*. It appears to have been correctly equated with *Nerita* rather than *Neritina* by Pilsbry, who had also studied its radula. Although *Fluvinerita* may be safely dismissed from further consideration as a possible relative of *N. ortoni*, it is of some interest as another example of a monospecific subgenus with no known close relatives.

Jung (1965: 480; pl. 62, figs 12, 13) identified a single specimen from the rich marine fauna of the Burdigalian (Zone N8) Cantaure Formation of the Paraguana Peninsula, northern Venezuela as *Neritina* aff. *woodwardi* Guppy (1866). This is now tentatively assigned to *N. ortoni*. Guppy's type specimen of *N. woodwardi*, from the Neogene of Jamaica, should be in BMPD (reg. no 64080) but appears to be lost. However, his illustrations (1866: 291; pl. 18, figs 4, 5) and those of Woodring (1928: 424; pl. 35, figs 7, 9) show a very different higher-spired shell, with a strongly curved columella on which the denticles are obscure. Jung's Venezuelan specimen has a low spire and flaring aperture. Above all, its comparatively velatiform apertural features resemble those of *N. ortoni*, though the angular junction between the callus pad and the base of the shell is not so sharp. A further difference is that the colour patterning is of a type not found in *N. ortoni*. Nevertheless, this Venezuelan specimen must be regarded as being very close to the Pebasian species, even if not conspecific.

Neritina is rare in the non-marine Neogene deposits of the Cuenca Basin, Ecuador (Bristow & Parodiz 1982: 34–37; BMPD collections), and, as Parodiz pointed out, none of the Cuenca species resemble the Pebasian fossils. Records of Neogene Neritidae from marine strata in South America and the Caribbean region are sparse (Canal Zone of Panama, Woodring 1957: 67; Dominican Republic, Maury 1917: 152; Venezuela, Weisbord 1962: 116). The subfamily is as yet unknown from the rich marine faunas of Peru and Ecuador described by Olsson in numerous papers, and in BMPD collections from Ecuador. A probable explanation for its rarity is that shells of sublittoral species have a greater chance of fossilization than those, such as *Neritina*, living either in the littoral zone or in fresh to brackish water.

Order **CAENOGASTROPODA** Cox, 1959
Superfamily **RISSOACEA** Gray, 1847

[Family Rissoina Gray, 1847: 150; Family Rissoidae, H. & A. Adams, 1854: 327; *nom. transl.* Thiele, 1929: 136]

Family **HYDROBIIDAE** Stimpson, 1865

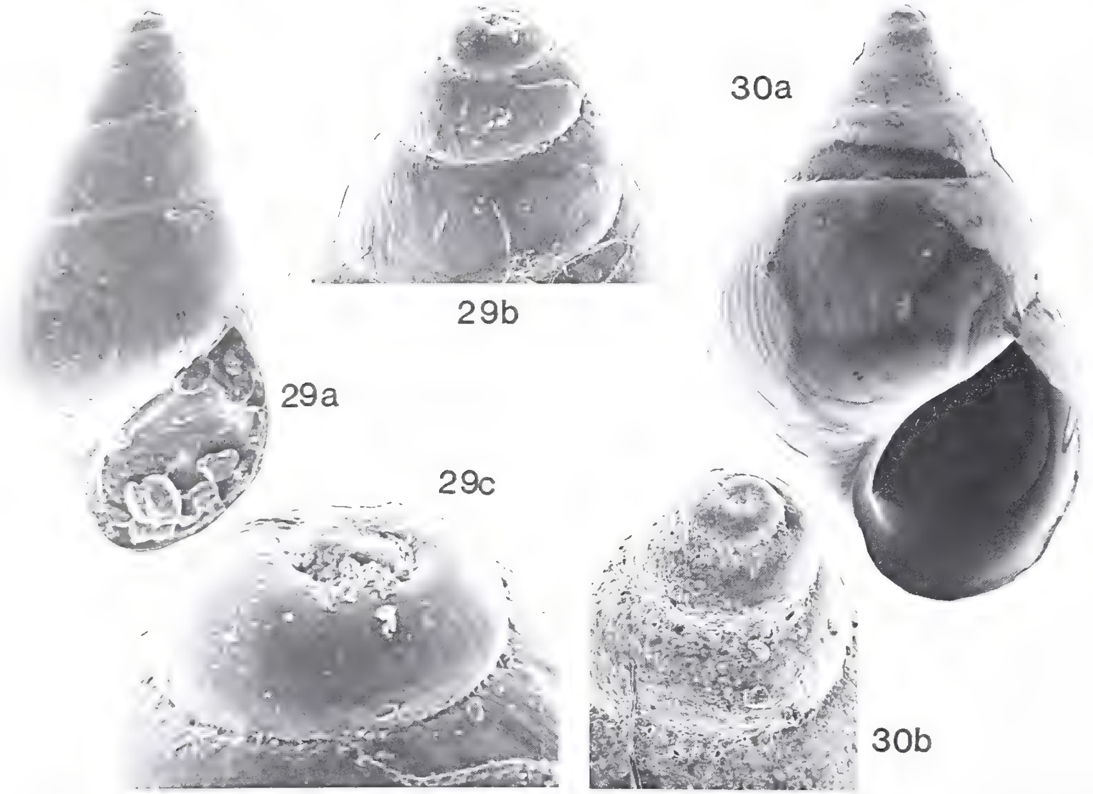
[Subfamily Hydrobiinae Stimpson, 1865*a*: 52, 1865*b*: 4, 39; *nom. transl.* Fischer, 1885: 725; = Paludestrinidae Newton, 1891: 226]

The assignment of fossil taxa to various subfamilies is perforce based entirely on shell characters. Several of these fossils do not fit comfortably into the taxonomic arrangements proposed in Taylor (1966), Davis & Pons da Silva (1984), Thompson (1984) and Hershler (1985).

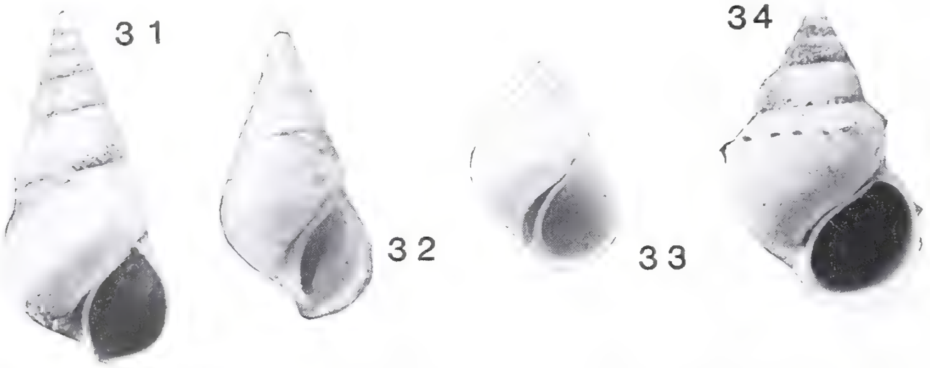
Subfamily **LITTORIDININAE** Thiele, 1928

[Tribus Littoridineae Thiele, 1928: 378; 1929: 141; *nom. transl.* Wenz, 1939: 571; = Subfamily Littoridininae 'nov.' Taylor, 1966: 182]

Taylor (1966), when proposing the Littoridininae as a new subfamily, was obviously unaware of its previous recognition (Wenz 1939, following Thiele, 1928). Paludestrinidae Newton (1891) was an unnecessary substitute name (see Cossmann, 1921: 95) for Hydrobiidae. Stimpson published Hydrobiinae twice in the same year: first, on 25 February, in the title only of his paper (1865*a*); in his second work (1865*b*), which appeared in August, full definitions were given. He did not mention *Littoridina* (type species by monotypy *L. gaudichaudi* Souleyet, 1852 (Fig. 39); Recent, Guayaquil, Ecuador), but in discussing *Paludestrina* d'Orbigny (1841: 8) proposed (1865*b*: 41) the name *Heleobia* for (Figs 31, 32) *Paludestrina culminea* d'Orbigny (1840: 36), almost certainly from Lake Titicaca, and its allies – species which subsequent authors have generally placed in *Littoridina*. *Heleobia* was treated as a synonym of *Littoridina* in Wenz (1939: 571), but has recently been resurrected by Davis *et al.* (1982: 168; Pons da Silva & Davis 1983: 131) for *Paludestrina australis* d'Orbigny and other species from Brazil, Uruguay and Argentina, on the grounds that their anatomy differs substantially enough from that described by Souleyet himself for *Littoridina gaudichaudi* to justify generic separation. No named specimens of *L. gaudichaudi* are available for comparison in BMZD. The type illustration of its shell, however, show it to be stouter and possibly with a heavier-lipped aperture than *Heleobia culminea* and the other South American species represented in BMZD. Thus, for the present, *Littoridina* is retained for its type species only, whilst all the smooth aciculate species which I have been able to examine and which are normally assigned to that genus – Taylor (1966: 182) estimated that there were about sixty living species – seem best accommodated in *Heleobia*. Haas (1955) erected several, mostly monotypic, new genera of Littoridininae from Lake Titicaca, apparently only on conchological grounds (collection, including types, in BMZD). The samples of all but *Brachypyrgulina* are very small. *Heleobia*, however, is abundant in the lake (BMZD colln). Both *Strombopoma* and *Rhamphopoma* (Fig. 32) Haas have shells typical of *Heleobia*, and *Heligmopoma* (Fig. 33) differs only in having a comparatively obtuse spire (spire angle 60°). *Brachypyrgulina* (Fig. 38) is characterized by its rectangular whorl profile, with a broad ramp and angular shoulder, whilst *Limnothauma* has a conical spire, a strong peripheral keel coinciding with the lower suture, and a broad, deep, umbilicus bordered by a basal keel. Hubendick, working on the anatomy of material from the same collection (1955: 322–326) reported that the verge, gill and radula of all of Haas's genera (with the exception of *Limnothauma*, which he did not examine and is known only by a single specimen)



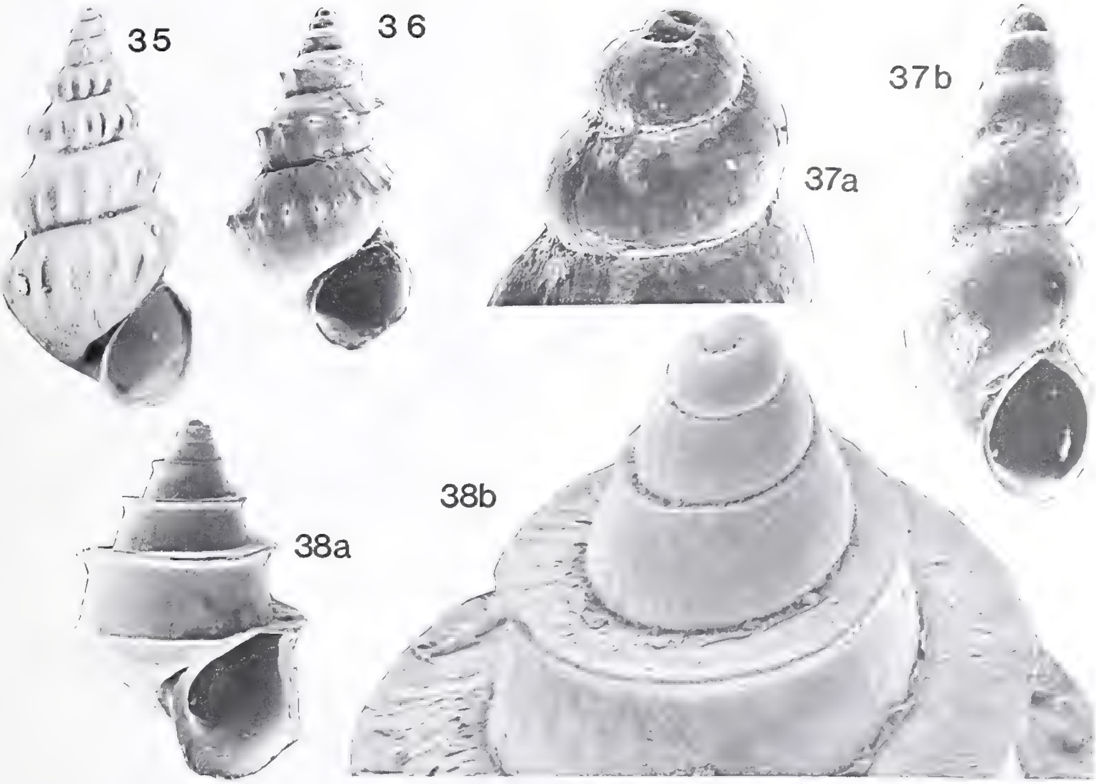
Figs 29–30 *Heleobia*. Recent, eastern Brazil. **29**a–c, *Heleobia australis* (d'Orbigny). BMZD 1958.4.10.7; front, × 20; early whorls, × 60; apex, × 200. Saco de Manguera, Rio Grande; E. C. Rios (Museo Oceanográfico de Rio Grande) Colln. **30**a, b, *Heleobia charruana* (d'Orbigny). BMZD 1984224; front, × 20; early whorls, × 60. Cananeir; given and determined by E. Marcus.



Figs 31–34 Recent Littoridininae. All in front view, × 8. **31**, *Heleobia culminea* (d'Orbigny). BMZD 1854.12.4.352, one of seven syntypes, labelled as holotype of *Paludestrina culminea* d'Orbigny. ? Lake Titicaca, Peru; d'Orbigny Colln, species no. 272. **32**, *Heleobia culminea* (d'Orbigny). BMZD 1956.xi.5.167, holotype of *Rhamphopoma magna* Haas; Chococoya, Lake Titicaca, depth 3.5 to 4.5 m. G. I. Crawford Colln. **33**, *Heligmopoma umbilicata* Haas. BMZD 1956.xi.5.157, holotype; Siripata Bay, Lake Titicaca, depth 2.4 m. G. I. Crawford Colln. **34**, *Potamopyrgus corolla* Gould. BMZD 1984225. Wanganui River, near Pipiriki, New Zealand.

had very uniform anatomy similar to that of *Littoridina* (i.e. *Heleobia*). He thought that though the operculae of *Strombopoma* and *Rhamphopoma* were of aberrant types, they might well have been derived from that of *Heleobia*. His conclusion (1955: 326) that these genera might have evolved in isolation in Lake Titicaca seems reasonable. This situation is probably analogous to the suspected adaptive radiation of the Thiaridae in Lake Tanganyika (see Wenz, 1939: 708–712).

Taylor (1966) placed some thirty high-spired species, including all the South American fossils originally described as *Dyris*, *Liris* and *Potamopyrgus*, into *Tryonia*, whose type species (Fig. 35) *T. clathrata* Stimpson (1865*b*), from the Pleistocene of Colorado, has rather sharp axial folds as well as the carinate whorl profile. The whorls of *Liris* have more evenly biconvex profiles, but the sculpture is similar to that of *Tryonia*. Taylor wrote that virtually all the species were known by their shells alone so that no 'trenchant characteristics' of the genus were possible. Thus, evidence for supraspecific classification is not available. There appear to be no sufficient reasons to accept that all these very differently sculptured species are congeneric as Taylor suggested. His approach seems somewhat inconsistent, for at the same time



Figs 35–38 Recent Littoridininae. **35**, *Tryonia clathrata* Stimpson, type species of *Tryonia*. BMZD 1900.6.26.1643. ? Pleistocene; Colorado, U.S.A.; × 12. **36**, *?Tryonia coronata* (Pfeiffer), usually referred to either *Pyrgophorus* or *Lyrodes*. BMZD 1984226. Recent; Venezuela; × 10. **37**a, b, *Durangonella mariae* Morrison, 1945. BMZD 1951.11.1.222, paratype; front, × 20; oblique view of apex, × 60. ?Subfossil; Tlahuac, D.F., Mexico; pres'd Smithsonian Institution. **38**a, b, *Brachypyrgulina carinifera* Haas. BMZD 1956.xi.5.102; paratype; front, × 12.5; oblique view of spire, × 50. Sucuné, Lake Titicaca, Peru, depth 5 m.

(1966: 179, 182 *et seqq*.) he accepted all of Haas' Lake Titicaca genera not only as distinct, but as belonging to two subfamilies, the Cochliopinae and Littoridininae. Moreover, *Tryonia* (*sensu* Taylor) would have a discontinuous geographical range (Taylor 1966: 183, text-fig. 14, map), and though the pre-Pleistocene record is sparse, Taylor's list (made without comment) implies that *Tryonia* was flourishing in both North and South America before the existence of the Panamanian land bridge.

The apparent adaptive radiations in Lakes Titicaca and Tanganyika may be taken as examples of what might be expected to occur in other groups, including fossils under consideration. There is, however, justification for the provisional classification of fossils on a slightly different, pragmatic, basis. None of the fossil species under consideration, including *'Littoridina' crassa* (Etheridge), can be confidently assigned to living genera of Littoridininae as listed in Taylor (1966: 182–3). In the present paper *Dyris* is used for those species with predominently spiral sculpture and *Liris* is retained for those with predominently axial, as opposed to collabral, sculpture. This generic arrangement is perhaps somewhat arbitrary and cannot claim to be more than a workable compromise. This is partly dictated by lack of knowledge of the Recent fauna. Both the small size of the available collections from such a vast region and the sparseness of the relevant literature suggest that small Mollusca of the Recent fauna have been relatively neglected. In addition, two other species, in particular, suggest not only a common ancestry but also a fairly close relationship between these two fossil genera. The type species of *Dyris* and *Liris* are very obviously distinct. The rare bicarinate and unicarinate shells in the Pichana sample here identified as belonging to *D. gracilis* Conrad – the type species of *Dyris* – do, however, approach the non-carinate *Liris* in shell morphology. The spirally ribbed *Dyris semituberculata* sp. nov. (p. 196) from La Tagua has weak and variable collabral folding, whilst *Dyris tuberculata* (de Greve 1938) from Iquitos has strong spiral and

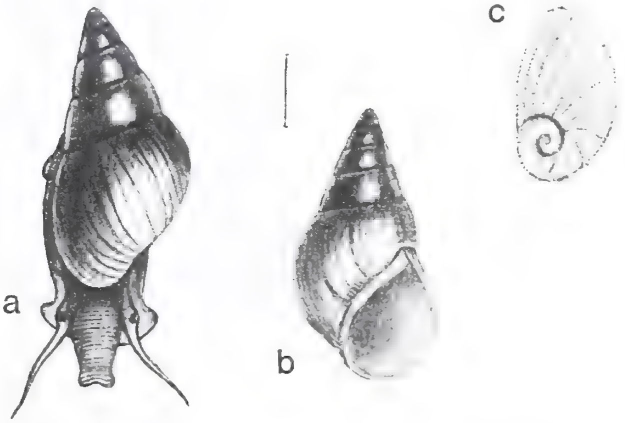


Fig. 39 *Littoridina gaudichaudi* (Souleyet). Recent; Guayaquil, Ecuador. Type illustrations copied at original size from Souleyet's (1852) figs 31–33; magnifications approximate. a, dorsal view of shell with live animal extended, × 3.75; b, ventral view of shell, × 3.75; c, operculum, × 6.

collabral sculpture. De Greve had assigned the latter species to *Liris* on the grounds that the peristome was detached from the body whorl as in the two other species occurring at Iquitos. This feature was also regarded as a generic distinction by Parodiz (1969: 119). However, this phenomenon is almost exclusively confined to Iquitos shells. It is linked with the spire angle reducing with growth, so that mature shells tend to be more acute, and is also often associated with the aperture being comparatively rounded as opposed to the normal tear-shape. *Liris* is thus a good example of how change in one character – in this case an increase in the whorl translation rate – may affect several others. The rather sporadic incidence of both detached peristomes and rounded apertures argues against either being a specific, let alone a generic, distinction.

To summarize, lack of comparative material makes it impracticable to postulate relationships between the various fossil and Recent genera. For example, it is accepted that the relationship between *Heleobia* and *Dyris* may be no more profound than that between *Heleobia* and *Brachypyrgulina*. In addition to *Heleobia*, favoured candidates as possible living relatives of the fossil genera include (Fig. 36) the Argentine *Lyrodes* (Doering 1884), the largely Central American *Pyrgophorus* (Ancey 1888) which is known from northernmost South America (Taylor, 1966: 194–196), and *Durangonella* (Morrison 1945) from Central Mexico (Fig. 37). *Lyrodes* is considered as distinct and characterized by fine spiral lirae: its type species, *L. guaranitica* Doering (subsequent designation by Pilsbry, 1911: 562) from Argentina, however, was placed in *Heleobia* (Pons da Silva & Davis 1983: 129).

Littoridininae range from fresh water through brackish (mangrove swamps and coastal lagoons) to marginal marine conditions, where they have been reported in association with genera such as *Brachydontes, Neritina, Nassarius* and *Thais* (Gaillard 1974*a*, *b*; Marcus & Marcus 1963*a*: 33, 1963*b*: 45–47).

Genus *DYRIS* Conrad, 1871

[= *Isaea* Conrad, 1871*b*, *non* Edwards, 1830; = *Conradia* Wenz, 1925, *non* A. Adams, 1860].

TYPE SPECIES. *Dyris gracilis* Conrad, 1871*b*; Late Caenozoic, Pebasian; Pichana, Peru. By monotypy.

DIAGNOSIS. Like *Heleobia*, but with predominantly spiral ribbing; peristome not detached.

OTHER SPECIES ASSIGNED. *Mesalia ortoni* Gabb, 1869, Pebas; *Isaea lintea* Conrad, 1871*b*, Pichana; *Hydrobia (Isaea) tricarinata* Boettger, 1878, Pebas; *Liris tuberculata* de Greve, 1938, Iquitos; *Dyris hauxwelli* sp. nov. (p. 192), Pichana. All Late Caenozoic, Pebasian, Upper Amazon Valley. *Potamopyrgus laciranus* Pilsbry & Olsson, 1935, Miocene, La Cira Formation, Upper Magdalena Valley, Colombia; *Dyris semituberculata* sp. nov. (p. 196), Late Caenozoic, La Tagua, Colombia.

GENERIC DISTRIBUTION. ? Neogene only, north-western South America. Unknown living.

REMARKS. The possible relationships between *Dyris* and living Littoridininae are discussed under the subfamily, above. Comparisons between *Dyris* and the living *Lyrodes* are discussed under *D. lacirana* (Pilsbry & Olsson), p. 195. Parodiz (1969) treated *D. gracilis, D. lintea* and *D. tricarinata* as conspecific, stating that he could observe clinal variation between the three in a sample from Três Unidos, and adding that the same variations could be observed in the numerous illustrations of Iquitos shells (de Greve 1938). It has now been possible to examine over 70 newly extracted shells from the sediment collected by Hauxwell from Pichana, as well as previously separated specimens in BMPD, which were presumably named by Woodward, and also the types of Conrad's two species, neither of which has been adequately illustrated before. This study suggests that, at Pichana, it is possible to recognize as distinct not only the three species named above, but also *D. hauxwelli* sp. nov. Further justification for separation is that the various species occur in different proportions – or in some cases, not at all – at different localities. The only quantitative guide to the relative rarity of these species at Pichana was afforded by the residue of matrix. When this was searched for the first time (additional specimens were obtained later in a subsequent search), the number of specimens obtained was as follows: *D. gracilis* (5), *D. lintea* (19), *D. tricarinata* (40), and *D. hauxwelli* (10). The original BMPD samples from Pichana (Woodward 1871: 102, 108, postscript) contain over fifty *D. tricarinata* and only seven fragments of *D. lintea*. Both *D. gracilis* and *D. hauxwelli* are absent: the former probably because of its rarity and the latter probably because of its small size. In contrast, at Iquitos, from the number of illustrations – de Greve gave no specimen counts in his text – it would appear that *D. lintea* and *D. tuberculata* are the two most common species. The other species appear to be rare at Iquitos, and the picture is further complicated by reidentifications herein. Thus *D. lintea* of de Greve (*pars*) = *D. gracilis*; *D. gracilis* of de Greve = *D. hauxwelli*. Although de Greve recorded *D. tricarinata* as occurring at Iquitos, it may be uncommon there, as his only illustrations of the species are of Boettger's types from Pebas.

Dyris gracilis Conrad, 1871 Figs 41–48, 454–455

*v 1871*b* *Dyris gracilis* Conrad: 195; pl. 10, fig. 8; pl. 11, fig. 7.
. 1878 *Hydrobia (Isaea) gracilis* (Conrad) Boettger: 493.
1879 *Dyris gracilis* Conrad; Etheridge: 86.
v. 1879 *Melania bicarinata* Etheridge: 88; pl. 7, fig. 7.
v. 1879 *Melania tricarinata* Etheridge: 87; pl. 7, fig. 6.
. 1926 *Hydrobia* (*Conradia*) *gracilis* (Conrad); Wenz: 1970.
? 1938 *Hydrobia (Conradia) lintea* (Conrad); de Greve: 83 (*pars*); pl. 1, figs 29, 30 (*non* figs 10, 28)
. 1966 *Tryonia bicarinata* (Etheridge) Taylor: 196.
. 1966 *Tryonia gracilis* (Conrad) Taylor: 197.
. 1969 *Dyris gracilis* Conrad; Parodiz: 118 (*pars*).

LECTOTYPE. Selected herein: NYSM 9192a, with height 5.9 mm. The accompanying NYSM 9192b, with height 4.9 mm, is a paralectotype. Both Late Caenozoic, Pebasian, Pichana (Hauxwell Colln). Holotype GG22421 (*ex* 97728) of *Melania tricarinata* Etheridge; Late Caenozoic, Canamá, Peru; Barrington Brown colln.

Lectotype (selected herein) GG22416 and two accompanying paralectotypes GG22417–8 (all *ex* 97724) of *Melania bicarinata* Etheridge; Late Caenozoic, Canamá, Peru; Barrington Brown Colln.

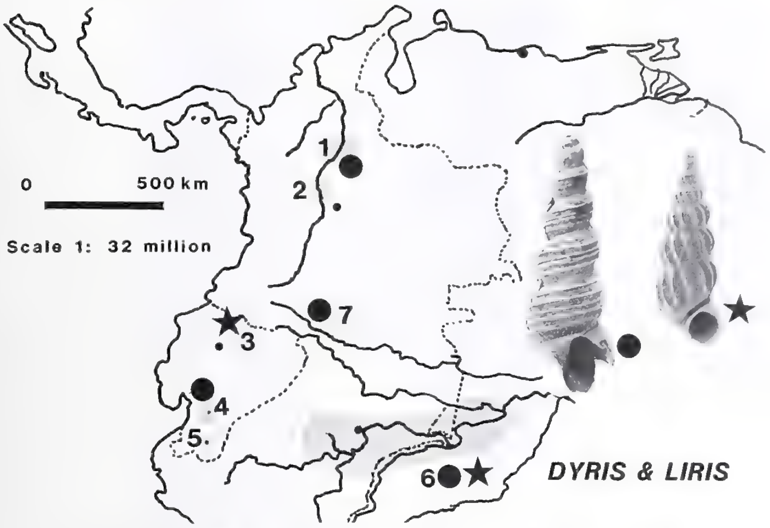
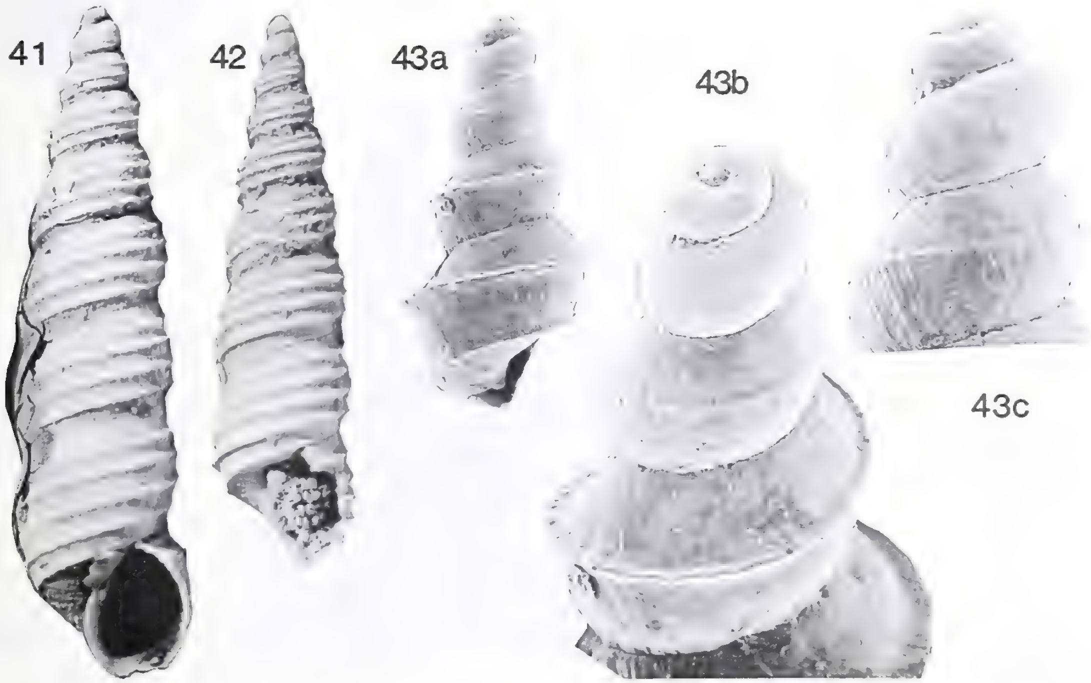


Fig. 40 Distribution of the extinct genera *Dyris* and *Liris*. Key as in Fig. 6, p. 177. ● = *Dyris;* ★ = *Liris*. Inset: left, *Dyris gracilis* Conrad, Pichana, Peru; right, *Liris scalarioides* (Etheridge); Puerto Nariño, Colombia.



Figs 41–43 *Dyris gracilis* Conrad. Pebasian; Pichana, Peru; Hauxwell Colln. **41**, NYSM 9192a, **lectotype** (herein selected), × 15. **42**, NYSM 9192b, paralectotype, × 15. **43**, GG19798: a, side view, × 40; b, oblique view of apex and spire whorls, × 100; c, side view of apex, × 100.

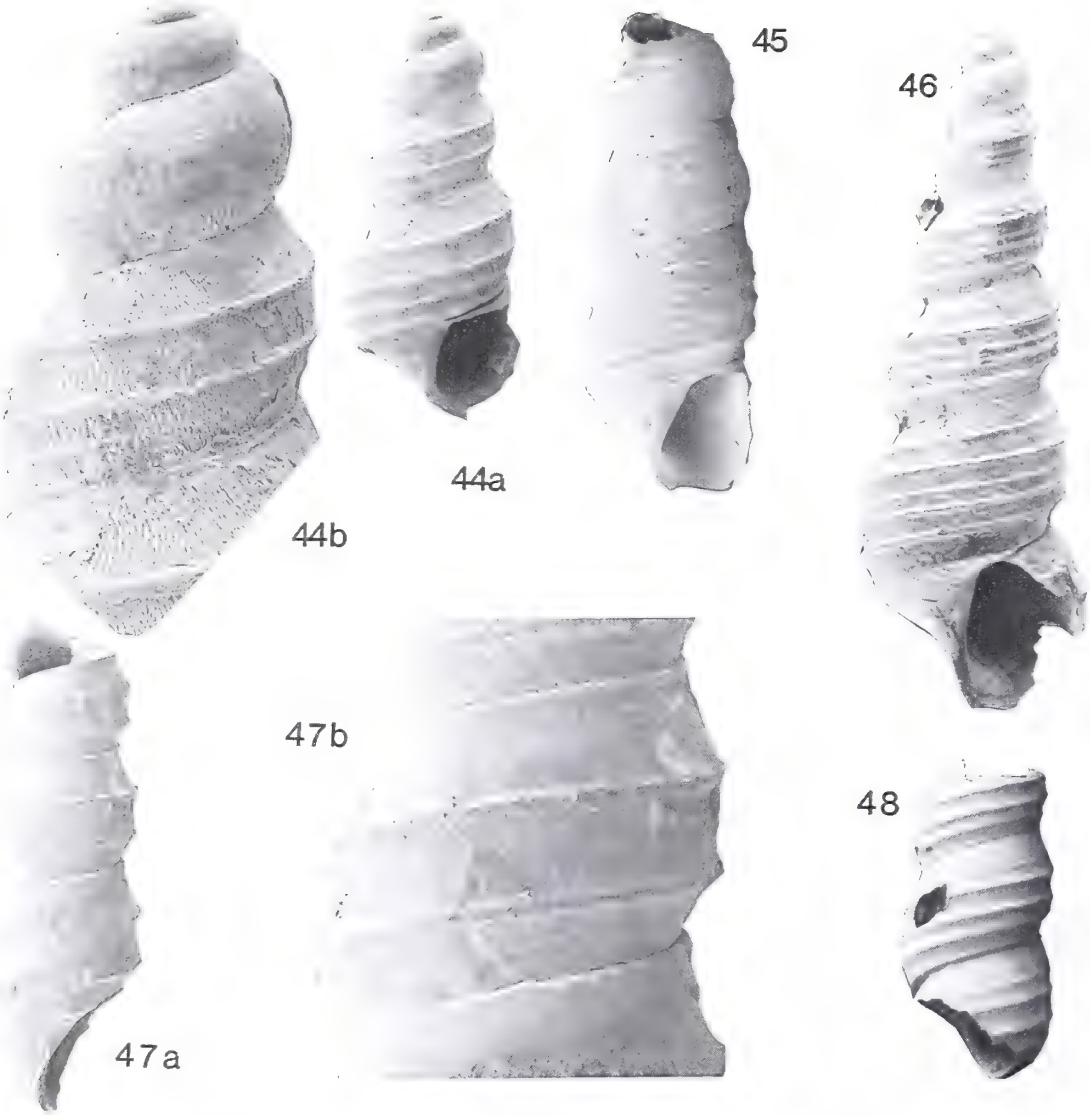
Other material studied. GG19796–8, GG21521–6, Late Caenozoic, Pebasian, Pichana (Hauxwell Colln, extracted 1982); GG21520, Puerto Nariño, Colombia (Weeda Colln).

Further occurrences. All Late Caenozoic, Pebasian. Pebas (Boettger 1878); Iquitos (de Greve 1938).

Diagnosis. Slender *Dyris* with a spire angle of between 13° and 17° bearing one to three fairly evenly spaced carinae, usually increasing to four or five on later whorls; aperture as little as a sixth of shell height.

Description. The tall apex is variable in height, comprising 2–2½ convex whorls which are smooth except for prosocyrt growth lines. A noticeable feature of the apex is the alteration of sutural slope in individual specimens. The last apical whorl is normally rather bulbous, and on it, one or more carinae develop at more or less the same time.

These are sometimes, but not always, joined fairly soon by up to three extra carinae. The carinae are sharp and separated by wide, concave, interspaces. Throughout growth a fairly distinct ramp and wide suprasutural groove persist, so that the whorl profile remains basically bicarinate. The growth lines change from prosocyrt on the apical whorls to reverse sigmoid on the later whorls and are more or less orthocline on the central portion of the whorl. In all shells, an additional carina marks the edge of the base of the whorl and is nearly or completely obscured by the following whorl, so that the sutural region is virtually smooth. The inner lip is just detached from the base, which is slightly concave and smooth except in one specimen, which bears a single weak spiral rib on its base.



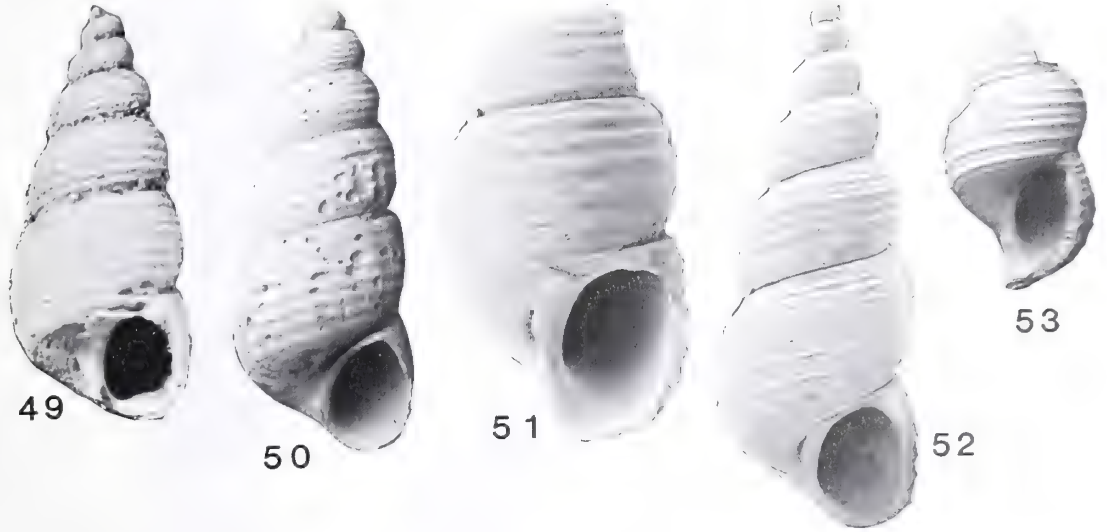
Figs 44–48 *Dyris gracilis* Conrad. Pebasian. **44–47**, Pichana, Peru; Hauxwell Colln. **44**, GG19797; a, front view, × 40; b, front view, early whorls only, × 100. **45**, GG21522; front view, × 15. **46**, GG19796; small specimen (h = 2.34 mm) resembling lectotype, × 40. **47**, GG21521; a, side view, × 15; b, penultimate whorl showing reverse sigmoid growth lines, × 50. **48**, GG21520; side view, × 15. Puerto Nariño, Colombia; Weeda Colln.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Lectotype, NYSM 9192a, Pichana	5.9	1.5	1.2	3.9	15°
Paralectotype, NYSM 9192b, Pichana	4.9	1.4	–	3.5	15°
GG19796, Pichana	2.3	0.8	0.5	3.0	17°
PIMUZ 833, Iquitos (fig'd de Greve 1938: pl. 1, figs 29, 30, as *H. lintea*)	7.7	2.2	1.7	3.5	–
Lectotype, GG22416, of *Melania bicarinata* Etheridge, Canamá	4.8+	1.4	1.4	–	18°
Holotype, GG22421, of *Melania tricarinata* Etheridge, Canamá	5.2	1.5	–	3.5	18°

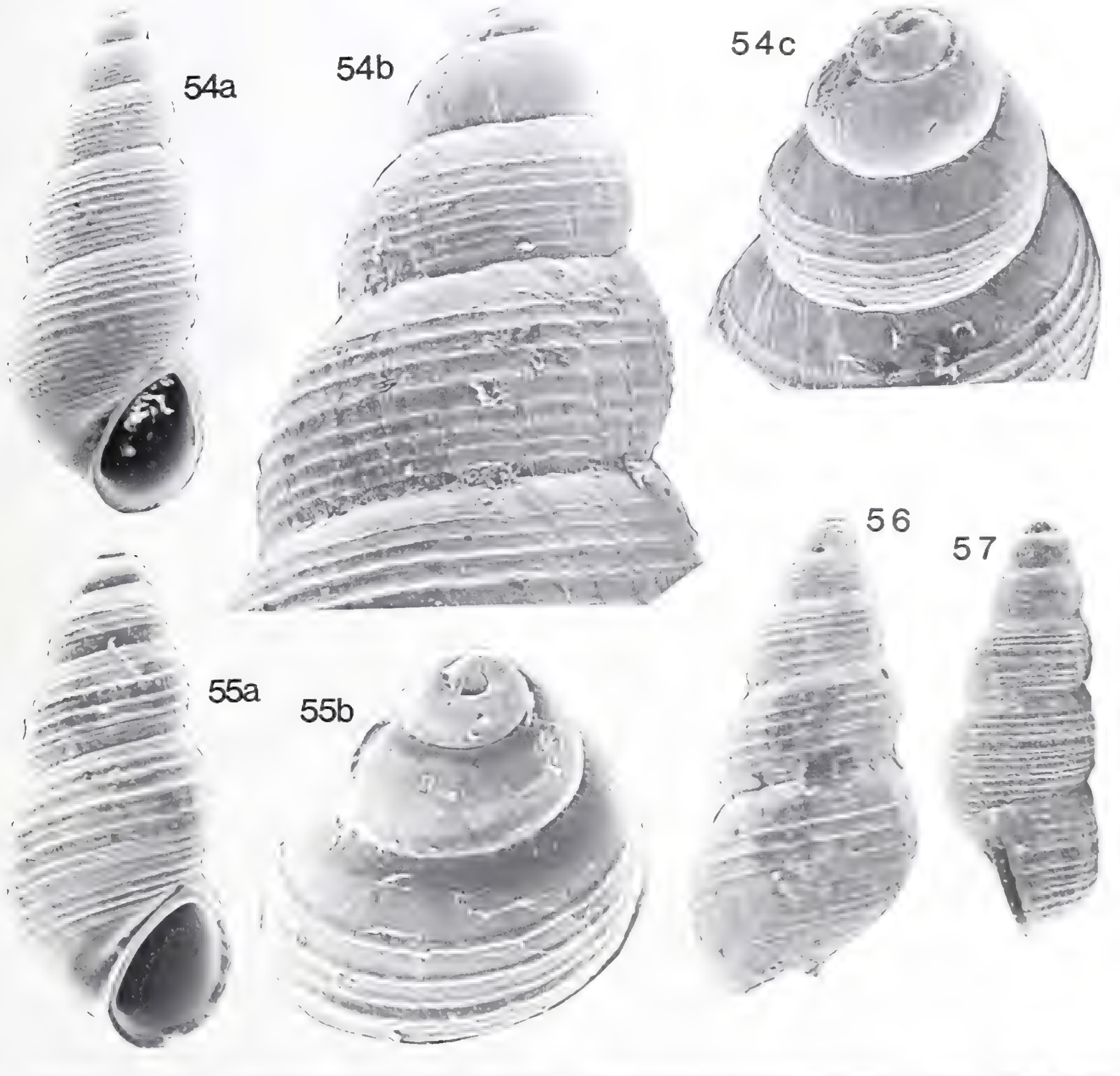
Note. Nearly all BMPD specimens are too fragmentary to measure.

REMARKS. This is a very rare species represented at Pichana mainly by broken fragments. Parts of the synonymy must be treated with suspicion because Conrad's original illustrations are so small as to be useless by themselves. However, coupled with his description, which includes the statement that there are four carinae on the penultimate whorl and five (i.e. including the basal) on the last, it is reasonable to assume that NYSM 9192 is the type series. Boettger's (1878) reference seems convincing. Roxo (1924: 48), who was quoted in de Greve's (1938) synonymy, was, in fact, remarking that he had *not* found the species at Três Unidos.

All specimens in BMPD of *Dyris lintea* (Conrad) are spirally multistriate. De Greve, however (1938: pl. 1, figs 10–30), figured a series of shells exhibiting considerable variation in spiral sculpture as that species. PIMUZ 833 (1938: pl. 1, figs 29, 30) is here referred to *D. gracilis* because of its few spiral ribs, even though they are comparatively weak, and in spite of its basal disc being neither concave nor bordered by a spiral carina. De Greve (1938: pl. 3, figs 21–28) identified as *D. ? gracilis* shells here referred to *D. tricarinata* (Boettger),



Figs 49–53 *Dyris lintea* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. **49**, NYSM 9252, holotype; × 10. **50**, GG19794; × 10. **51**, G45294; × 15. **52**, G25293; × 15. **53**, GG19795; × 10.



Figs 54–57 *Dyris lintea* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. **54**, GG19790; a, front view, × 30; b, c, side and oblique views of early whorls, × 100; note prominent growth line on second whorl, possibly marking position of aperture of larval shell. **55**, GG19791; a, front view, × 30; b, oblique view of apex, × 100. **56**, GG19792; rear view, × 30. **57**, GG19793; side view, × 30.

whilst his pl. 5, figs 30 and 37 are now assigned to *D. hauxwelli* sp. nov. (see p. 192). The distinctions between *D. gracilis* and *D. hauxwelli* are given under the latter. *D. tricarinata* (Boettger) may be easily separated from *D. gracilis* by its larger apical whorls, greater spire angle and different whorl profile.

Dyris lintea (Conrad, 1871) Figs 49–58

*v 1871 *Isaea lintea* Conrad: 193; pl. 10, fig. 6.
. 1878 *Hydrobia (Isaea) lintea* (Conrad) Boettger: 493.
. 1924 *Isaea lintea* Conrad; Roxo: 49.
. 1926 *Hydrobia (Conradia) lintea* (Conrad); Wenz: 1970.
. 1938 *Hydrobia (Conradia) lintea* (Conrad); de Greve: 83 (*pars*); pl. 1, figs 10–28 (*non* figs 29, 30).
. 1966 *Tryonia lintea* (Conrad) Taylor: 197.
. 1969 *Dyris gracilis* (Conrad); Parodiz: 118 (*pars*).
. 1980 *Hydrobia lintea* (Conrad); Costa: 879; pl. 1, figs 5, 6.
. 1981 *Hydrobia lintea* (Conrad); Costa: 639; pl. 1, figs 3, 4.

HOLOTYPE. NYSM 9252, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln).

OTHER MATERIAL STUDIED. All Late Caenozoic, Pebasian. G25293–7, Pichana, Peru (Hauxwell Colln); GG19790–5, GG21676–9, GG21680/1–5, Pichana, Peru (Hauxwell Colln, extracted 1982); GG19961, GG21519, GG21681–5, Puerto Nariño, Colombia (Weeda Colln).

FURTHER OCCURRENCES. All late Caenozoic, Pebasian. Pebas (Boettger 1878); Três Unidos (Roxo 1924, Costa 1981); Iquitos (de Greve 1938); CPCAN I, Tamanduá, CPCAN II, Poreré, CPCAN III, São Paulo de Olivença, Afloramento em Italaia do Norte (Costa 1980). Upper Amazon Basin only.

DIAGNOSIS. *Dyris* up to 16 mm high with evenly convex whorls; sculptured with between six and ten spiral ribs per whorl on early whorls; later whorls with spiral grooves.

DESCRIPTION. The description of the early whorls is based on the newly extracted juveniles from Pichana, as all the adults are damaged. The apex of 2–2¼ whorls is naticiform and has a height and breadth of about 0.3 mm. Spiral ribbing develops rapidly on the next whorl and the full number of ribs is developed by the sixth whorl. There are 9–10 whorls in all. The spiral ribs are narrow and separated by convex interspaces. The arrangement of the ribbing is normally fairly regular and of even strength, but more variation is shown in de Greve's illustrations (1938) of Iquitos shells and also in the specimens from Puerto Nariño.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Holotype NYSM 9252	5.5	2.4	*c.* 1.3	2.25	30°
G25293	5.1	2.1	1.4	2.43	30°–38°
G25294	3.8	1.6	–	–	–
G25295	2.7	–	–	–	38°
(penultimate whorl)		(1.1)			
GG19790	2.40	0.95	0.76	2.53	25°
GG19791	2.25	1.00	0.67	2.25	–
GG19792	2.15	1.00	–	2.15	28°
GG19793	1.87	0.71	–	2.63	–
GG19961	10.5 (e 15+)				18°
GG21519	6.4 (e 12+)	3.2	–	–	–

All Pichana, except GG19961, GG21519 (Puerto Nariño).

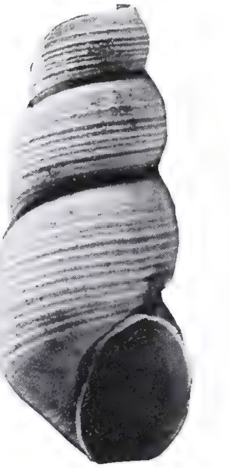


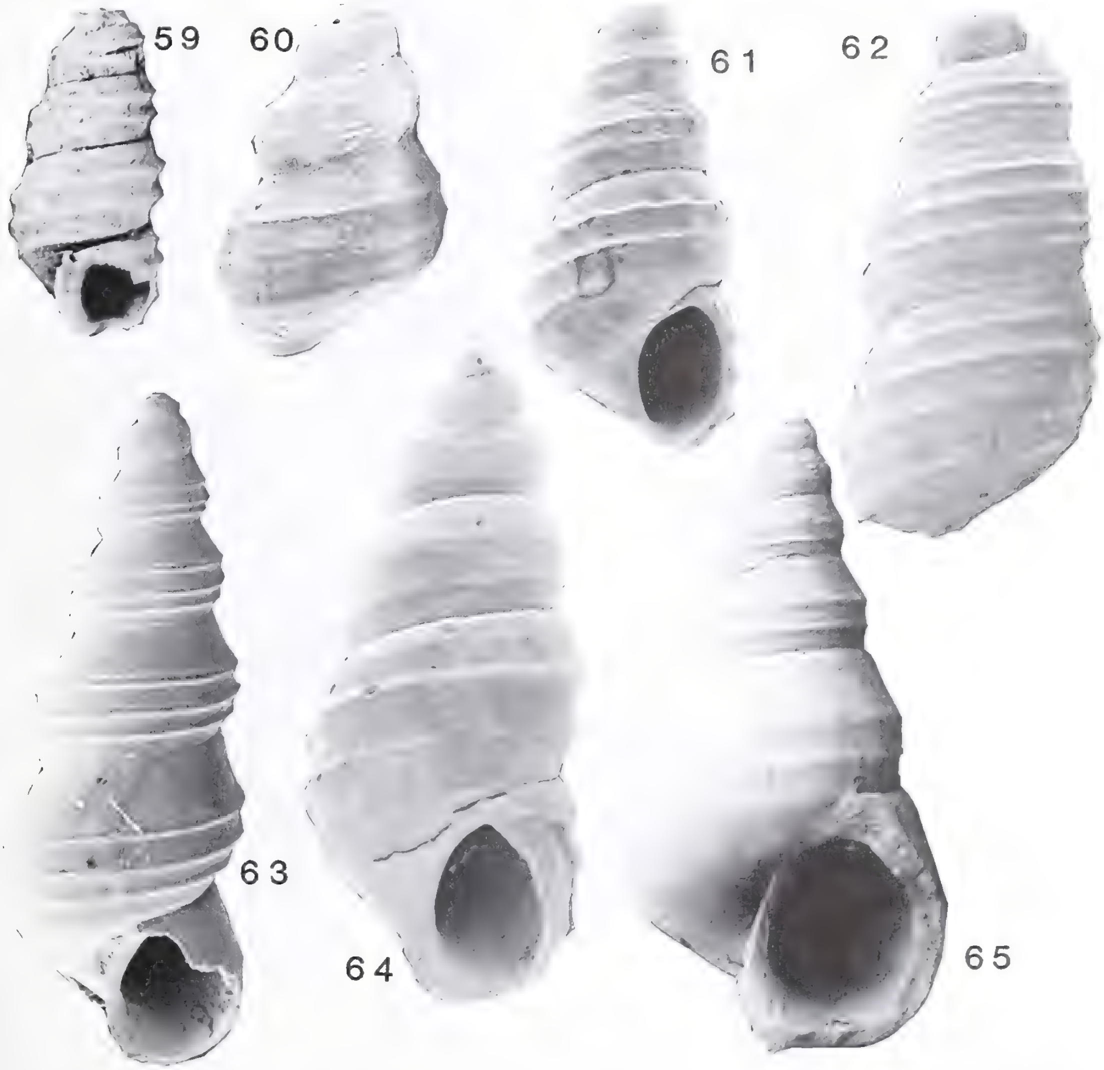
Fig. 58 *Dyris lintea* (Conrad). Pebasian; Puerto Nariño, Colombia; Weeda Colln. GG19961; front view, × 6.

REMARKS. Careful examination suggested that the newly extracted, and often almost perfectly preserved, small shells from Pichana belonged to this species, otherwise known only from rather incomplete adults, all of which, including the worn holotype, lack the early whorls. The penultimate whorl of GG25295 has a breadth of 1.1 mm and both its profile and sculpture appear very similar to those of the specimens here considered to be only partly grown. The large shells from Puerto Nariño are also referred to this species: the typical spiral ribbing is exhibited on the early whorls of GG19961 (Fig. 58), though this is replaced by spiral grooving on later whorls of both this specimen and GG21519. But these determinations, both of the small Pichana shells and the large Puerto Nariño specimens, cannot be regarded as definite because of the lack of well preserved specimens providing a continuous view of how the sculpture develops. Elsewhere, *D. hauxwelli* sp. nov. is separated from the co-occuring *D. tricarinata* (Boettger). The apical whorls of both are preserved and it is clear that the former is a much smaller species. It is felt that the specimens available provide no similar grounds to justify splitting into two species the large and small individuals here all assigned to *D. lintea*.

D. lintea is easily distinguished from other known species of *Dyris* by its more numerous spiral ribs and the fact that they are fairly evenly dispersed over the whorl surface of the spire whorls, which are evenly biconvex. Aciculate specimens of this species most closely resemble *D. gracilis* Conrad, but in the latter the spiral sculpture may be described as consisting of sharply crested carinae, which are less numerous than the ribs of *D. lintea*.

Dyris tricarinata (Boettger, 1878) Figs 59–78

v. 1871*b* *Isaea ortoni* (Gabb) Conrad: 193 (*pars*); pl. 10, fig. 10 (*non* pl. 10, fig. 13)
v. 1871 *Isaea tricarinata* Conrad; Woodward: 108 (*nom. nud*).
*. 1878 *Hydrobia (Isaea) tricarinata* Boettger: 492; pl. 13, figs 10a, b, 11a–c.
. 1926 *Hydrobia (Conradia) tricarinata* Boettger; Wenz: 1971.
. 1938 *Hydrobia (Conradia) tricarinata* Boettger; de Greve: 81; pl. 1, figs 7–9.



Figs 59–65 *Dyris tricarinata* (Boettger). Pebasian; Pichana, Peru; Hauxwell Colln. **59**, shell figured by Conrad (1871*b*: pl. 10, fig. 10) as *Isaea ortoni* (Gabb), NYSM 9253; front view, × 10. **60**, GG21692; rear, × 25. **61**, GG21693; front, × 20. **62**, GG21690; rear, × 20. **63**, G25289; front, × 15; see also Fig. 66. **64**, GG21691; front, × 20. **65**, G25290; front, × 15.

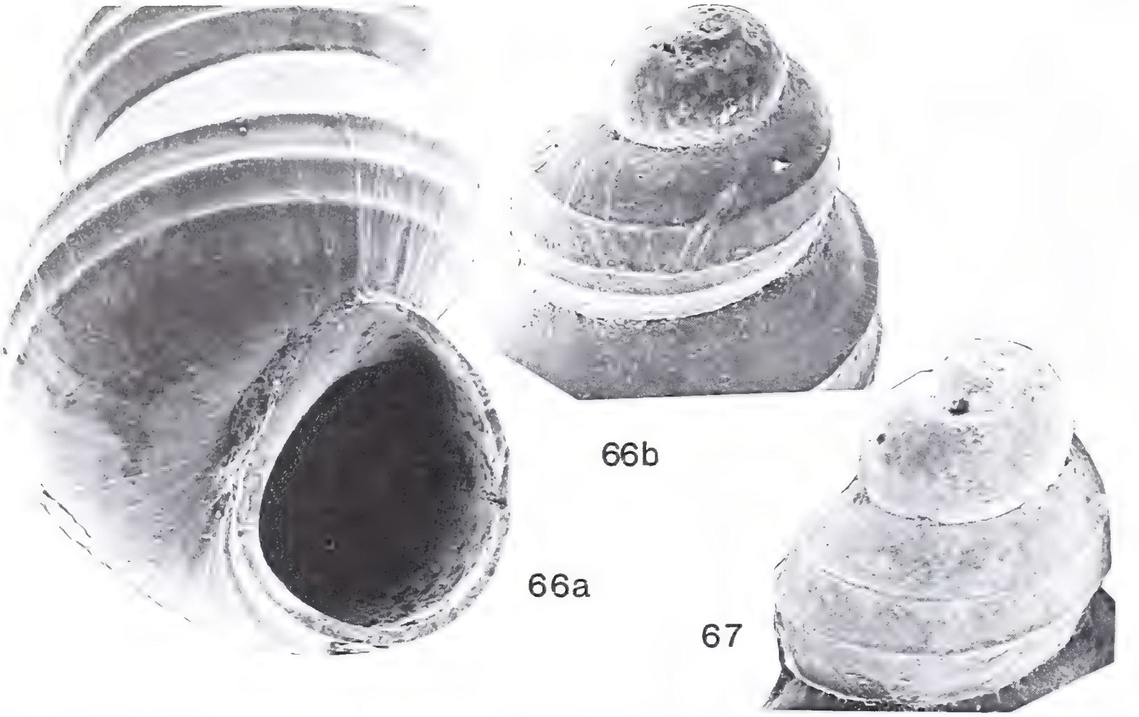
. 1966 *Hydrobia tricarinata* Boettger; Willard: 65; pl. 62, figs 4–6.
. 1966 *Tryonia tricarinata* (Boettger) Taylor: 197.
. 1969 *Dyris gracilis* Conrad; Parodiz: 118 (*pars*).
. 1980 *Hydrobia tricarinata* Boettger; Costa: 878; pl. 1, figs 5, 6.
v. 1982 *Dyris* cf. *gracilis* 'form' *carinata* (Boettger); Bristow & Parodiz: 16, 41.

TYPE MATERIAL. Types of *Hydrobia tricarinata* Boettger not studied. Senckenburg Museum, Frankfurt. One of Boettger's specimens (1878: pl. 13, fig. 11), was designated by de Greve (1938) as 'Typus' (= Lectotype) and another (1878: pl. 10, fig. 10) as Paratype. Both Late Caenozoic, Pebasian; Pebas, Peru.

MATERIAL STUDIED. Late Caenozoic, Pebasian: G25289–90, GG21686–8, GG21689/1–30, Pichana, Peru (Hauxwell Colln); GG21690–4, GG21695/1–20, Pichana, Peru (Hauxwell Colln, extracted 1982); NYSM 9253, six shells, including the shell figured by Conrad (1871: pl. 10, fig. 10), Pichana, Peru (Hauxwell Colln); GG21527–9, Puerto Nariño, Colombia (Weeda Colln). Late Caenozoic: GG19840–9, GG19958, 1.5 km upstream from La Tagua, Colombia (Weeda Colln); GG19936, Loc. 33, 480–560 cm, La Tagua (Eden Colln); GG19929–32, Loc. 54, La Tagua (Eden Colln). ? Upper Miocene (Bristow & Parodiz, 1982: 17), San Cayetano Formation, Loja Basin, Ecuador: GG19809, GG21706–15, Loc. JW 424, Grid ref. 008 582 (Bristow & Parodiz, 1982: 16, 41). G43325–6, Loja (Prof C. Carrion Colln, 1926) are in similar matrix and are probably from the same horizon.

FURTHER OCCURRENCES. Late Caenozoic, Pebasian: Pebas (Boettger 1878, de Greve 1938); CPCAN III, São Paulo de Olivença (Costa 1980); Iquitos (de Greve 1938, Willard 1966). Três Unidos (Roxo 1924) is doubtful. Late Caenozoic, Pebasian, Upper Amazon Basin; Late Caenozoic, La Tagua, Colombia; Loja Basin, Ecuador.

DIAGNOSIS. *Dyris* with large blunt apex; lower half of subsequent whorls sculptured with two or three, or rarely more, prominent spiral carinae; upper half of whorl forming broad, smooth, steeply sloping ramp.



Figs 66–67 *Dyris tricarinata* (Boettger). Pebasian; Pichana, Peru; Hauxwell Colln. **66**, G25289; a, oblique view of apertural region, × 30; b, oblique view of apex, × 66; see also Fig. 63. **67**, GG21692; oblique view of apex, × 50.

DESCRIPTION. The apex consists of 2–2½ biconvex whorls which rapidly increase in size, and are smooth except for opisthocyrt growth lines. Spiral sculpture of sharp, coarse ridges or carinae quickly develops and, in the next whorl or so, these strengthen to superimpose the very variable but basically bicarinate adult whorl profile upon the biconvex smooth profile of earlier whorls. Perhaps the most constant feature is the ramp which occupies virtually all the adapical half of the whorl and slopes steeply at 60°–70°. In some specimens from La Tagua the spiral ribs are more numerous but weaker, so that the profile reverts to biconvex for the last whorl or so. In a small proportion of shells from Pichana the spiral carinae are of irregular strength, giving a slightly frilly appearance. The peristome is rimmed and sometimes slightly detached.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Lectotype, Pebas (from de Greve, 1938)	5.3	2.25	1.5	2.36	21°
G25289, Pichana	5.8	2.2	1.5	2.32	22°
G25290, Pichana	6.2	3.1	2.0	2.0	45°
GG19936, La Tagua, 33/480–560 cm	5.5	2.2	1.4	2.1	25°
GG19840, 1.5 km upstream from La Tagua	4.9	2.2	1.4	2.23	28°
GG19841, as above.	5.3	2.2	1.5	2.4	28°
GG19842, as above.	4.4	1.2	–	3.67	25°
GG21528, Puerto Nariño.	3.2	1.6	–	2.0	26°
GG21527, Puerto Nariño.	2.8	1.4	–	2.0	26°

REMARKS. De Greve (1938), when designating types, refigured Boettger's (1878) type material from Pebas, but none of his own from Iquitos. De Greve's measurements are highly suspect: he gave two views of the lectotype at different magnifications, but neither agrees with the dimensions that he gave (1938: 83) in his text and which are quoted here. Conrad thought that this species was the young of *Mesalia ortoni* Gabb (see Fig. 59) and, in response to this, the five shells originally registered as G25290 were originally labelled '*Isaea tricarinata* Conrad, possibly the young of *I. ortoni*': this is the sample discussed by Woodward (1871: 108, PS). Boettger, who was aware of the views of Conrad and Woodward, validated the name.

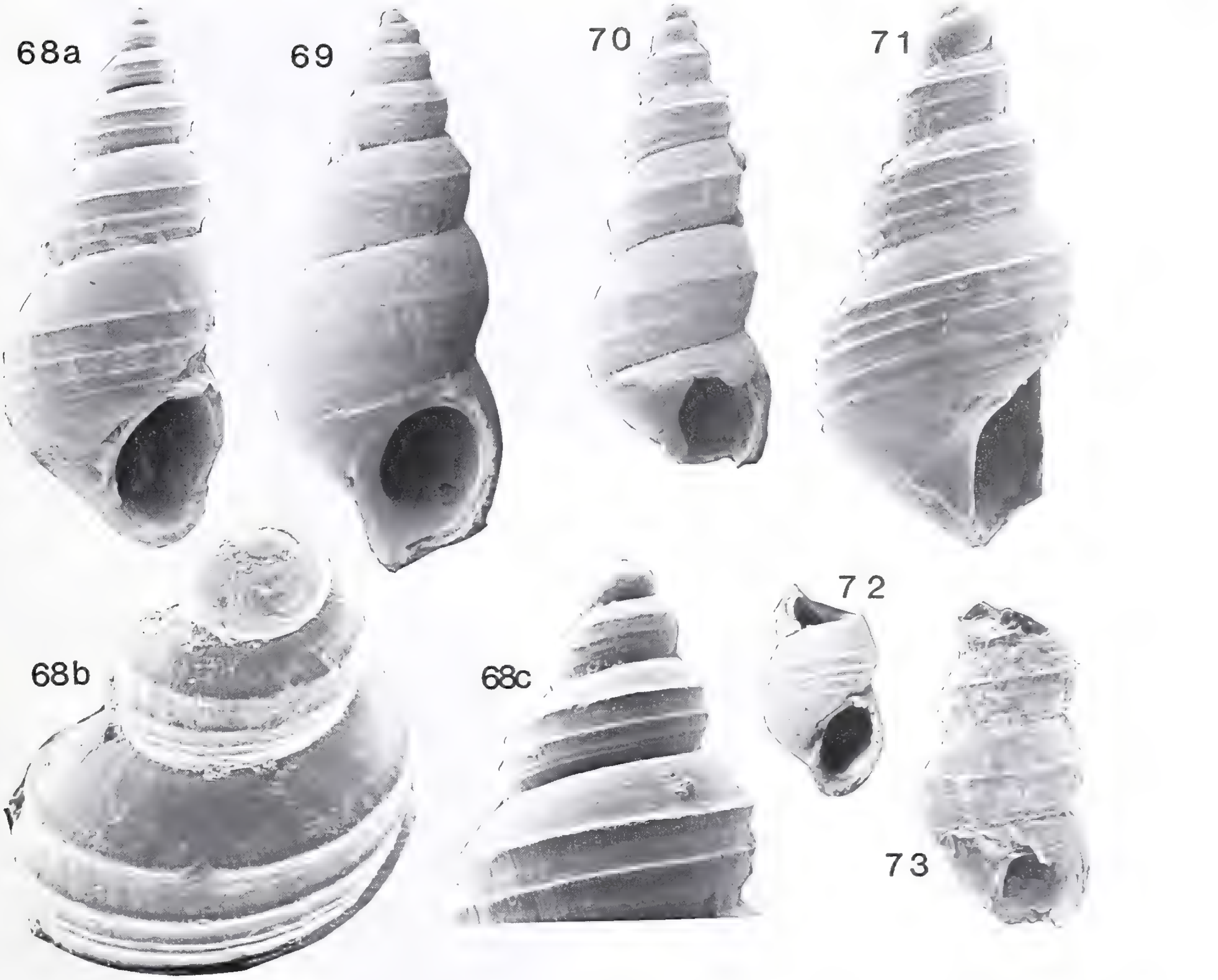
Three other species, *D. lacirana* (Pilsbry & Olsson), *D. semituberculata* sp. nov. (p. 196), and *D. hauxwelli* sp. nov. (below), are similar to *D. tricarinata* in that their spiral ribbing is confined to the lower part of the whorl. *D. lacirana* is known only from poorly preserved material but apparently has a more rounded whorl profile with the ramp less well differentiated, partly because of its weaker ribbing and partly because the ramp itself is slightly convex rather than concave. *D. semituberculata* from La Tagua is distinguished by its collabral folds which produce a much more frilly effect than seen in a small proportion of specimens from Pichana. *D. hauxwelli* is much smaller, with smaller apical whorls and a distinctly biconic whorl profile.

The material (GG18909, GG21706–15, GG43325–6) from the San Cayetano Formation, Ecuador, consists of numerous external moulds on bedding planes in a fine marl. No other species are known to occur in these samples. These specimens are referred to *D. tricarinata* on their size (up to 5 mm in height) and on the character of their ribbing, though their whorl profiles appear to be more pagodiform or biconic than that of the typical Pebasian material. This may, however, be the result of distortion and the fact that sections on bedding planes are seldom sagittal.

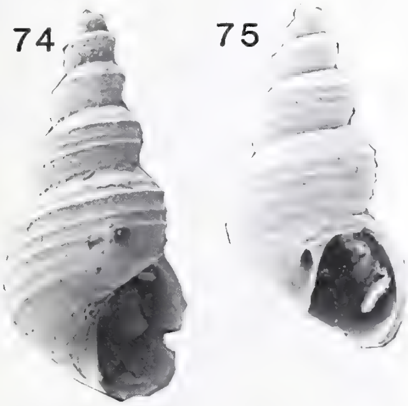
Roxo's record (1924) of the species from Três Unidos is treated as doubtful because it was not confirmed in either of Costa's two recent papers (1980, 1981).

Dyris hauxwelli sp. nov. Figs 79–85

v. 1871*b* *Isaea ortoni* (Gabb); Conrad: 193 (*pars*).
v. 1938 *Dyris (?) gracilis* Conrad; de Greve: 86; pl. 3, figs 21–28; pl. 5, figs 30, 37.
v. 1939 *Dyris gracilis* Conrad; Wenz: 572, fig. 1548.



Figs 68–73 *Dyris tricarinata* (Boettger). Late Caenozoic; La Tagua, Colombia. **68–70**, 1.5 km upstream from La Tagua; Weeda Colln. **68**, GG19840; a, front, × 15; b, oblique view of apex, × 75; c, side view of early whorls, × 40. **69**, GG19841; front, × 15. **70**, GG19842; × 15. **71–72**, Loc. 54; Eden Colln. **71**, GG19930; × 40. **72**, GG19929; × 12. **73**, GG19936; × 15; Loc. 33/480–560; Eden Colln.



Figs 74–75 *Dyris tricarinata* (Boettger). Pebasian; Puerto Nariño, Colombia; Weeda Colln. **74**, GG21527; front, × 20. **75**, GG21528; front, × 15.

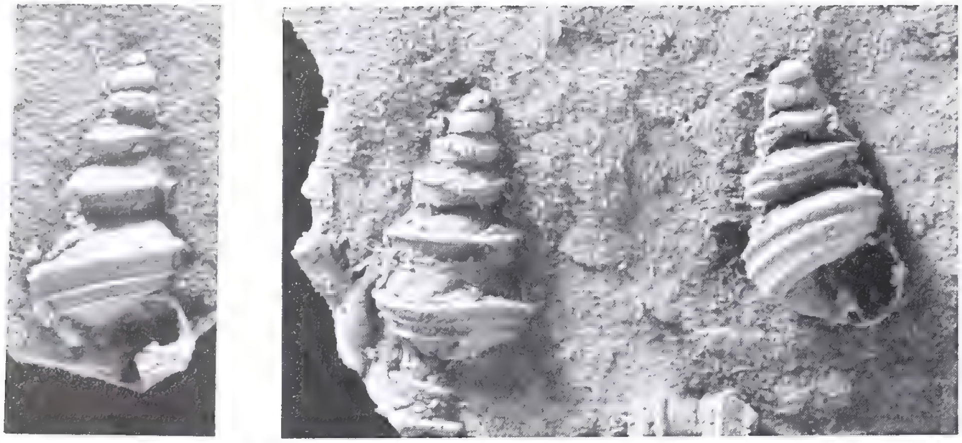
HOLOTYPE. GG19792, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln, extracted 1982). The following are paratypes; all Late Caenozoic, Pebasian. GG19793, GG21627–9, GG21696–705, Pichana, as above; NYSM 9253, one of seven shells misidentified by Conrad as *Isaea ortoni* (Gabb) – the remaining six are now reidentified as *D. tricarinata* (Boettger). GG19799, GG19960, Canamá (C. Barrington Brown Colln, extracted 1982); PIMUZ 491A, unfigured by de Greve (1938); PIMUZ 497C, de Greve, pl. 5, fig. 30 which was copied by Wenz (1939: fig. 1548); PIMUZ 491B, de Greve, pl. 5, fig. 37, all Iquitos. No other records.

NAME. From Juan Hauxwell's Collection, purchased by the BM in 1870.

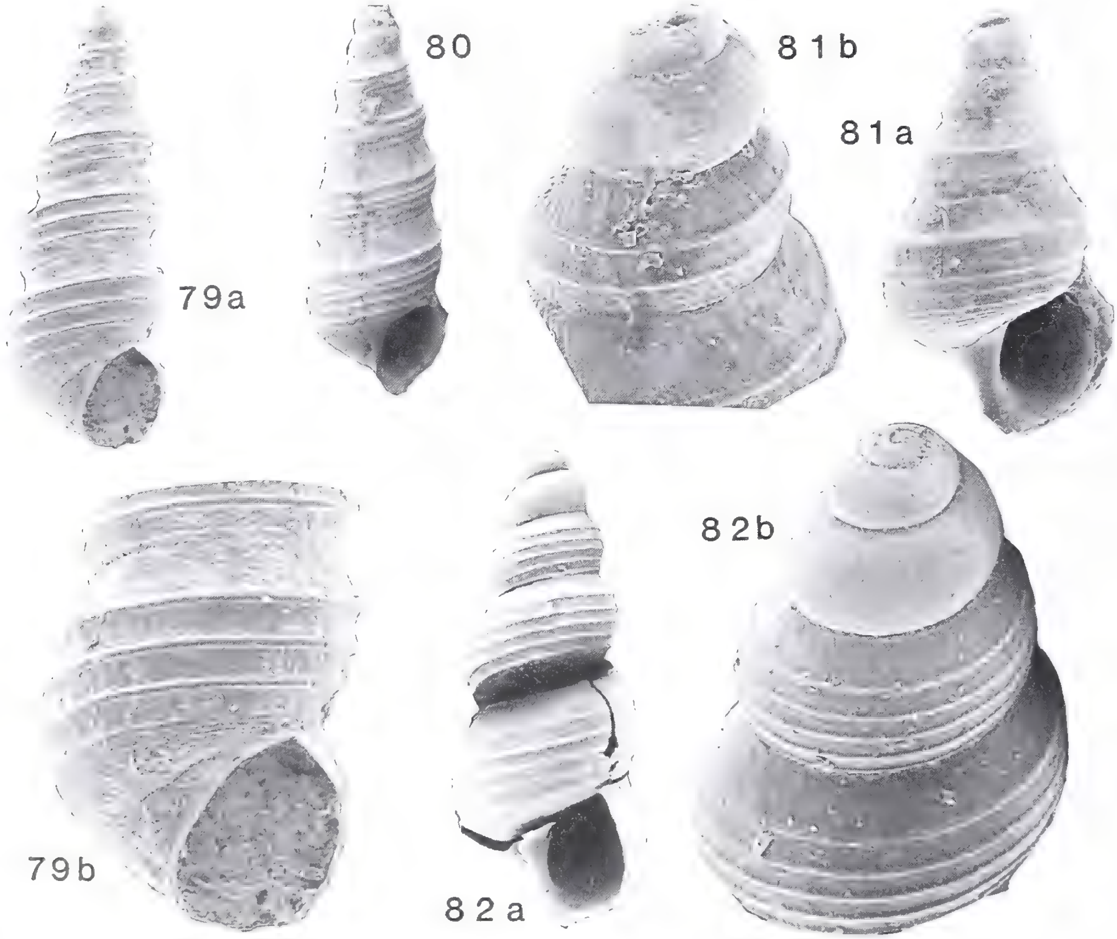
DISTRIBUTION. Late Caenozoic, Pebasian only. Upper Amazon basin only.

DIAGNOSIS. Like *Dyris tricarinata*, but much smaller, attaining the same number of whorls in half the height and with a markedly pagodiform whorl profile.

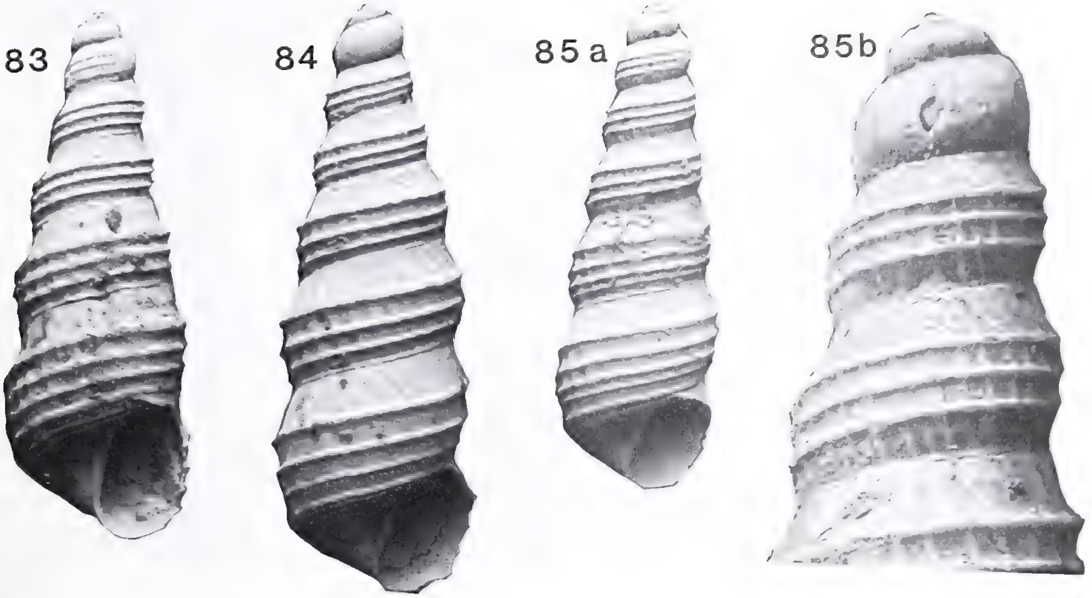
DESCRIPTION. This species has a height of under 3 mm and has about eight whorls. The spiral ribs, which are first seen on the third whorl, are relatively prominent for its size; that at the periphery is normally the strongest and those below it are progressively weaker towards the abapical suture. There are normally three or four ribs on each whorl but a small proportion of Pichana shells and the two from Canamá have five or six. Very weak threads can be seen on the base of the body whorl of the Iquitos shells and on some of those from Pichana. On the Iquitos shells, some of the growth lines are sufficiently strong to produce the appearance of collabral ribbing.



Figs 76–78 *Dyris tricarinata* (Boettger). San Cayetano Formation, presumed Miocene; Loc. JW 424, Loja Basin, Ecuador; all × 10. **76**, GG21706. **77**, GG21707. **78**, GG21708.



Figs 79–82 *Dyris hauxwelli* sp. nov. Pebasian. **79–81**, Pichana, Peru; Hauxwell Colln. **79**, **holotype**, GG19792; a, front, × 25; b, apertural region, × 50. **80**, paratype, GG21627; front, × 25. **81**, GG21628; a, front, × 40; b, oblique view of apex, × 100. **82**, GG19799; Canamá, Peru; Barrington Brown Colln. a, front, × 40; b, oblique view of apex, × 75.



Figs 83–85 *Dyris hauxwelli* sp. nov. Pebasian; Iquitos, Peru; originally identified by de Greve (1938) as *Dyris gracilis* Conrad. **83**, PIMUZ 491a; front, × 30. **84**, PIMUZ 491b, figured by de Greve (1938: pl. 5, fig. 37); front, × 30. **85**, PIMUZ 497c; a, front, × 30; b, apical whorls, × 75, figured by de Greve (1938: pl. 5, fig. 30).

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Holotype, GG19792, Pichana.	2.32	0.90	0.53	2.58	21°
GG21627, Pichana.	2.60	0.95	0.70	2.74	22°
GG21628, Pichana.	1.38	0.75	–	1.84	32°
GG21629, Pichana.	1.3	0.7	–	1.85	32°
GG19799, Canamá.	2.1	0.83	0.5	2.53	24°
PIMUZ 497C, Iquitos.	2.1	0.7	0.4	3.0	18°
PIMUZ 491B, Iquitos.	2.5	0.8	0.4	3.1	20°
PIMUZ 491A, Iquitos.	2.3	0.8	0.5	2.9	18°

REMARKS. The differences between similar species of *Dyris* with smooth ramps are discussed under *D. tricarinata* (Boettger), p. 192. No difficulty was encountered in separating *D. hauxwelli* from *D. tricarinata* in the newly extracted BMPD material from Pichana. It is probable that this small species has been overlooked by earlier workers and that it is more widespread than indicated here. For example, de Greve (1938) had separated his specimens from *D. tricarinata* but had identified them as *D.* (?) *gracilis*. Had he been able to examine the types of that very different species, he would probably have concluded that his material belonged to an undescribed species.

Dyris lacirana (Pilsbry & Olsson, 1935) Fig. 86

*v 1935 *Potamopyrgus laciranus* Pilsbry & Olsson: 9; pl. 5, fig. 6.
. 1966 *Tryonia lacirana* (Pilsbry & Olsson) Taylor: 197.
v. 1969 *Lyrodes laciranus* (Pilsbry & Olsson) Parodiz: 117; pl. 16, fig. 4 (a copy of the type illustration).

HOLOTYPE. ANSP 13074, Miocene, La Cira Formation; near Zopffs, La Cira district, Colombia (W. W. Waring Colln). The numerous accompanying specimens, all on blocks of indurated haematitic sandstone (co-occurring with paralectotypes of *Pachydon abundans* (Pilsbry & Olsson), herein placed in the synonymy of *P. cebada* (Anderson, 1928): see p. 311) are paratypes.

OTHER RECORDS. 'Also at many localities near La Cira' (Pilsbry & Olsson 1935: 9).

DISTRIBUTION. Only known from the La Cira Formation, as above. This formation was dated as either late Oligocene or early Miocene by Pilsbry & Olsson (1935), but is here regarded as Miocene.

DIAGNOSIS. *Dyris* with spiral ribs increasing from two to five with growth and confined to the lower half of whorl; whorl profile biconvex to weakly carinate at mid whorl-height.

DESCRIPTION. All the specimens are damaged: neither the apical whorls nor the aperture are properly known and the ribbing can only be examined on small, isolated, areas of shell surface. The spiral ribs, which are absent from the upper part of the whorl, are weak and increase in number from two or three on early whorls to five on the last whorl. On early whorls, the uppermost rib is just above the periphery but on later whorls it descends as low as the periphery. The whorl profile is usually evenly biconvex, though exceptionally the topmost rib forms a weak carina.

DIMENSIONS. In mm.	h	br	hap	sa
Holotype, ANSP 13074	3.9	1.8	–	30°

REMARKS. Comparisons with similar species are given under *D. tricarinata*, p. 192. The similarities are sufficient to suggest that this species should be assigned to *Dyris* as opposed to any of the genera used by previous authors. *Potamopyrgus* is based on a living New Zealand species, *Melania corolla* Gould, 1847. Its whorls are coronated with spines, and it seems unlikely that the genus occurs in South America. *Lyrodes* is widespread in South America at the present day

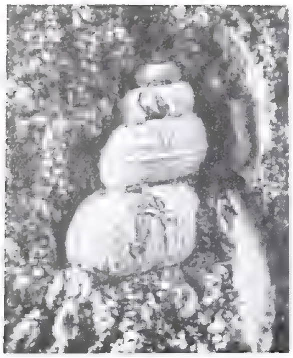


Fig. 86 *Dyris lacirana* (Pilsbry & Olsson). La Cira Formation, dated herein as Miocene; near Zopffs, Middle Magdalena Valley, Colombia; W. W. Waring Colln. Holotype, ANSP 13074; × 15. Note that the type illustration of Pilsbry & Olsson (1935: pl. 5, fig. 6) appears to be a reconstruction, and is probably based partly on this specimen.

(Parodiz 1969: 117). It differs from *Dyris* in being thinner-shelled, translucent and very finely spirally striate.

Pilsbry & Olsson's original figure was copied by Parodiz (1969). It is a reconstruction which cannot be matched with any of the ANSP specimens seen. It bears some resemblance to the specimen which has been isolated as holotype (ANSP 13074; Fig. 86) but this has one less whorl than the illustration. However, both the character of the ribbing and the whorl profile are accurately represented.

Dyris semituberculata sp. nov. Figs 87–102

Holotype. GG19853, Late Caenozoic; 1.5 km upstream from La Tagua, Colombia (Weeda Colln). The following are paratypes: GG19850/1–3 (juveniles), GG19854–5, GG21620–5, GG21626/1–10 (all as above); GG19937–9, GG19940/1–5, Loc. 54, La Tagua (Eden Colln); GG21716, GG21226–9, Loc. 33/480–560 cm, La Tagua (Eden Colln).

Name. Distinct from *tuberculata*, with less marked sculpture.

Diagnosis. *Dyris* with collabral sculpture on later whorls, consisting of about twenty folds or wrinkles per whorl; ramp smooth, with carinate shoulder below, both sometimes lost on later whorls as they become biconvex; spiral sculpture variable, up to about nine ribs per whorl.

Description. The sculpture is very variable and has a strong influence on the equally inconstant whorl profile. The first whorl is very small in comparison with the second which is bulbous, strongly biconvex, and twice as broad as high. The spiral sculpture first develops on the next whorl, as a carina with a broad ramp above. A second carina soon forms, thus making the whorl profile convexly bicarinate. Up to nine spiral ribs of varying strength may form on the spire whorls. As their number increases they tend to weaken and the whorl profile becomes biconvex with the periphery lying at mid whorl-height in most specimens. In some, however, a carinate shoulder with a comparatively smooth ramp above persists. About five more spiral ribs are present on the upper part of the base of the body whorl. Collabral sculpture does not appear until the fifth whorl and consists of low amplitude folds, often rather pinched at both sutures. The peristome is only lightly pressed against the body whorl, but is not detached. The base is usually almost umbilicate.

Dimensions. In mm.	h	br	hap	h/br	sa
Holotype, GG19853, 1.5 km upstream of La Tagua.	5.8	2.2	1.5	2.45	30°
Paratype, GG21716, Loc. 33/480–560, La Tagua.	5.5	2.5	1.4	2.2	–

Note. The majority of specimens are too incomplete to provide meaningful measurements.

Remarks. In *D. tuberculata* (de Greve), the collabral sculpture consists of much stronger but less numerous folds and its peristome is often detached. Juveniles of *D. semituberculata* and *D. tricarinata* (Boettger) are similar, but the early whorls of the new species are smaller and have a much more angular profile. A biconvex profile of later whorls is a common feature of *D. semituberculata* but rare in *D. tricarinata*. In the latter, the sculpture never develops such a strongly frilly appearance.

Dyris tuberculata (de Greve, 1938) Fig. 103

* 1938 *Liris tuberculata* de Greve: 96; pl. 2, figs 32–35; pl. 3, figs 1–20; text-figs 19–22.
. 1939 *Liris tuberculata* de Greve; Wenz: 572, fig. 1549 (copy of de Greve, pl. 3, fig. 10?).
1966 *Liris tuberculata* de Greve; Willard: 69, 93.
. 1966 *Tryonia tuberculata* (de Greve) Taylor: 197.
. 1969 *Liris tuberculata* de Greve; Parodiz: 120.

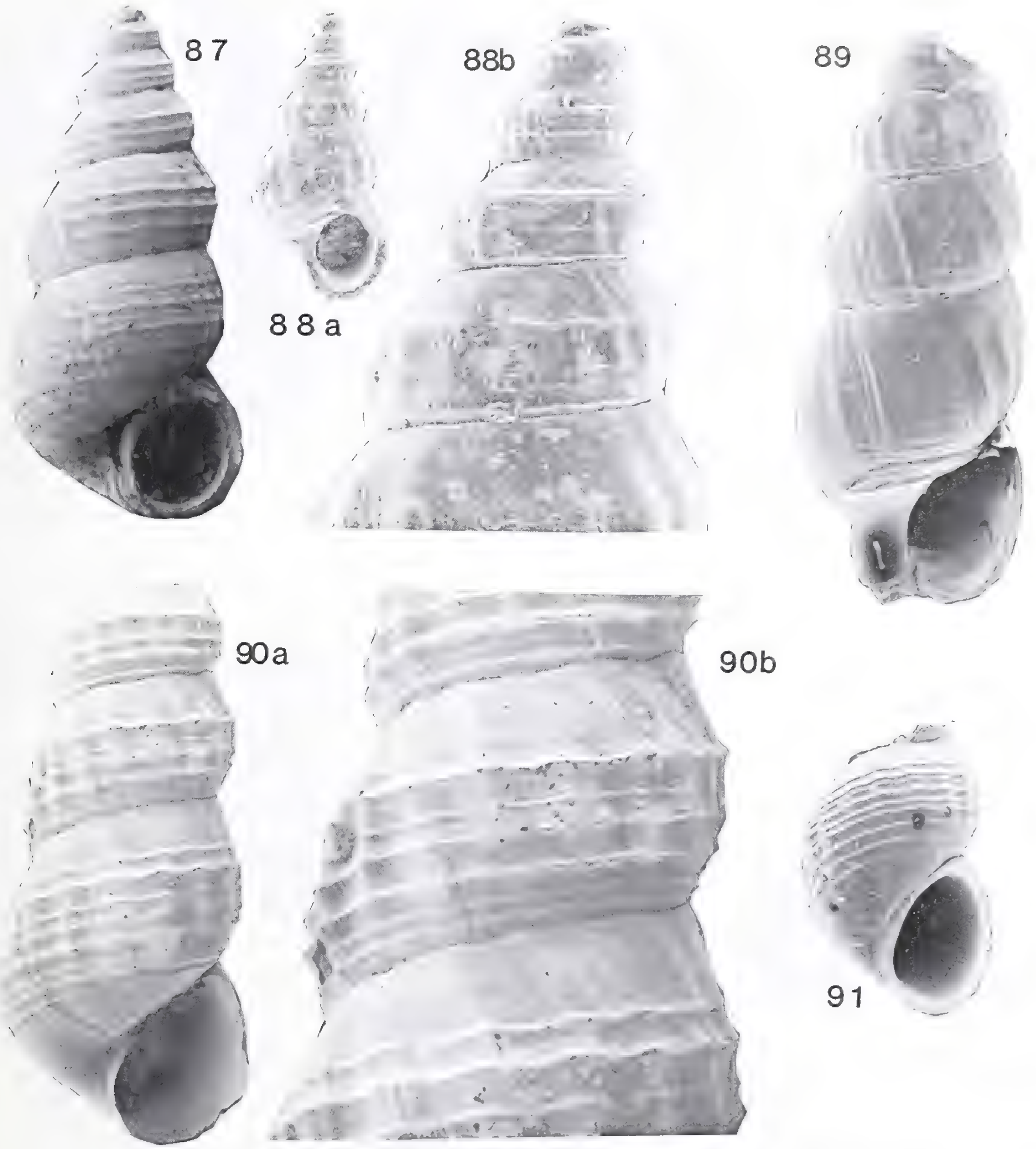
Holotype. PIMUZ 423, Late Caenozoic, Pebasian; Iquitos, Peru (de Greve 1938: pl. 2, figs 32–34) (Peyer Colln). About a dozen specimens (de Greve 1938), same details as holotype, are paratypes.

Other material. A specimen (Fig. 103) was found loose with PIMUZ 317, *Hemisinus kochi* (Bernardi) (p. 241), from Iquitos; same details as above.

Distribution. Late Caenozoic, possibly confined to Pebasian of Iquitos, Peru. A doubtful record is from the late Caenozoic, Rio Aguaytia, about 25 km from confluence with Rio Ucayali, *c.* 100 km south of Contamana (Willard 1966).

Diagnosis. *Dyris* with bicarinate whorls and 14–20 strong collabral ribs; peristome frequently detached.

Description. The spire angle decreases markedly with growth in individual shells and also varies between 14° and 34° within the species. The first two whorls are smooth, strongly biconvex, and tilted about 45° to the shell axis. Two weak spiral ribs are developed on the next whorl. The first traces of collabral sculpture consist of up to twenty nodes per whorl, set at regular intervals. By the fourth whorl these nodes develop into short collabral ribs in the peripheral region bounded by the two spiral carinae. On the fifth and sixth whorls, the collabral ribs gradually spread onto both the ramp and the lower part of the whorl. By the seventh whorl both the sculpture and the bicarinate whorl profile have assumed their adult form. Secondary spiral ribs are present. One occurs near the periphery, between the two spiral carinae;

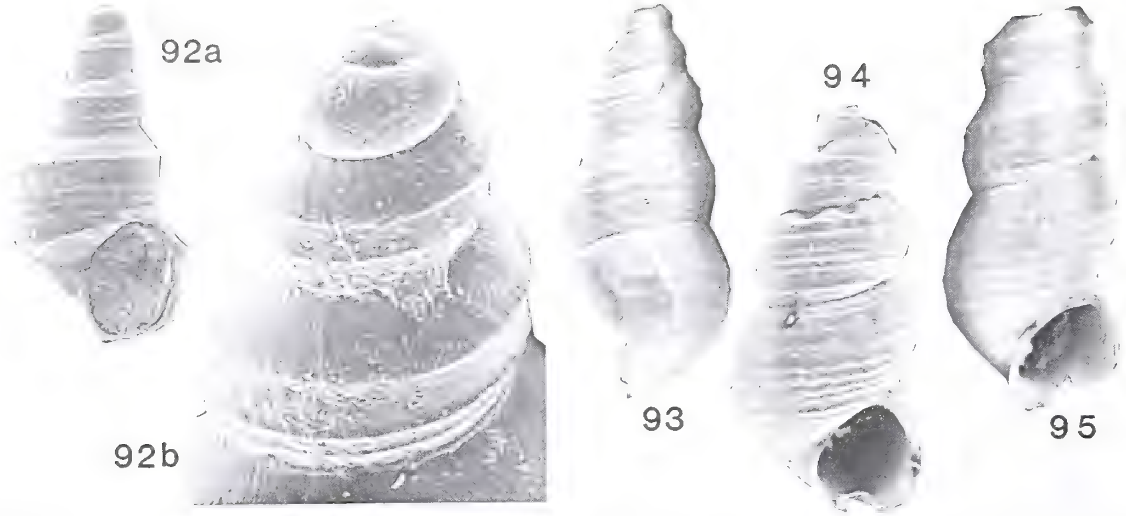


Figs 87–91 *Dyris semituberculata* sp. nov. Late Caenozoic; 1.5 km upstream from La Tagua, Colombia; Weeda Colln. **87**, **holotype**, GG19853; front, × 15. **88–91**, paratypes. **88**, GG21623; a, front, × 12.5; b, early spire whorls, × 50. **89**, GG21621; front, × 20. **90**, GG 19854; a, front, × 20; b, penultimate whorl, × 40. **91**, GG21625; front, showing undamaged aperture, × 10.

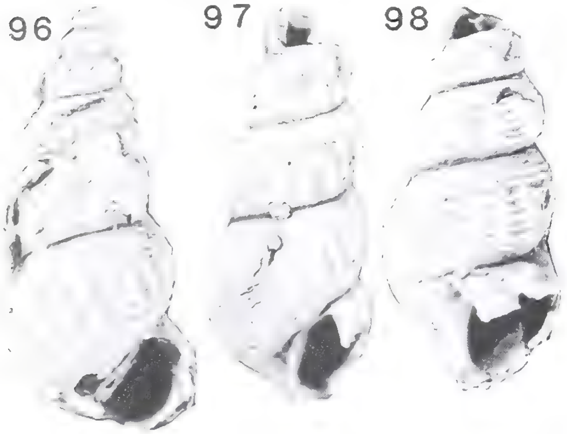
another quite strong rib lies between the lower carina and the lower suture. A further carina lies at the lower suture; it is only partly exposed, except on the body whorl of specimens with detached peristomes, when it is revealed to be extremely strong, forming a flange which separates the side from the base of the whorl. The *c.* 20 collabral nodes on the early whorls reduce to 14–16 collabral ribs on the later whorls. In section, these ribs are of an angular, zigzag pattern, except near both sutures where they broaden into low semiangular folds. As far as can be seen, the ribbing runs parallel to the growth lines, and is therefore collabral. The growth lines are weak, except on the base. In the single studied specimen, the sculpture is reduced in strength on the last whorl as it approaches the aperture. The base of the whorl is convex and lacks ribbing. The peristome is detached in some, but not all,

DIMENSIONS. In mm.	h	br	h/br	sa
PIMUZ 423, holotype (de Greve 1938: pl. 2, figs 32–34).	5.4 (4.6)	2.3	2.35	(30°–22°)
PIMUZ 418D (pl. 3, fig. 5).	5.5	1.9	2.89	(18°)
PIMUZ 430 (pl. 3, fig. 7).	5.5	2.3	2.39	(34°)
PIMUZ (studied herein).	4.6	1.65	2.79	22°

Note. Except for the un-numbered specimen studied herein, the figures are taken either from de Greve's (1938) text or from his plates; the latter are given in brackets. The discrepancies are particularly great in the case of the holotype.



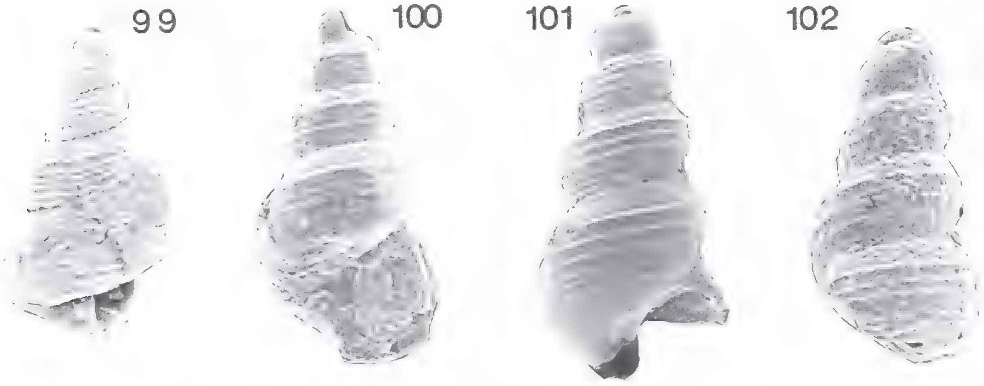
Figs 92–95 *Dyris semituberculata* sp. nov. Late Caenozoic; 1.5 km upstream from La Tagua, Colombia; Weeda Colln. Paratypes. **92**, GG21624; a, front, × 25; b, oblique view of early spire whorls, × 100. **93**, GG21622; side, × 15. **94**, GG19855; front, × 15. **95**, GG21620; front, × 15.



Figs 96–98 *Dyris semituberculata* sp. nov. Late Caenozoic; Loc. 54, La Tagua, Colombia; Eden Colln. Paratypes, all × 12.5. **96**, GG19937. **97**, GG19938. **98**, GG19939.

of the specimens figured by de Greve (1938). The rounded outer lip and semi-straight inner lip are joined below in an even curve and above at an angulation. The aperture tends to be more rounded in specimens with detached peristomes.

REMARKS. This species differs from *D. semituberculata* sp. nov. (p. 196) in having much stronger and more regular sculpture and fewer collabral ribs. *Liris tuberculata* de Greve is here transferred to *Dyris,* because of its apparent affinity with *D. semituberculata* and the close resemblance of its early whorls to those of specimens PIMUZ 491B and 497C from Iquitos. These were figured by de Greve (1938: pl. 5, fig. 37 and pl. 5, fig. 30, respectively) as *Dyris gracilis* Conrad, but are here reidentified as *D. hauxwelli* sp. nov. (p. 192). Although these specimens differ from ones from Pichana, the type locality of *hauxwelli*, in having prominent collabral striae they are unmistakably *Dyris* rather than *Liris*.



Figs 99–102 *Dyris semituberculata* sp. nov. Late Caenozoic; Loc. 33/480–560, La Tagua, Colombia. Paratypes. **99**, GG21226; × 20. **100**, GG21227; × 30. **101**, GG21228; × 40. **102**, GG21229; × 50.

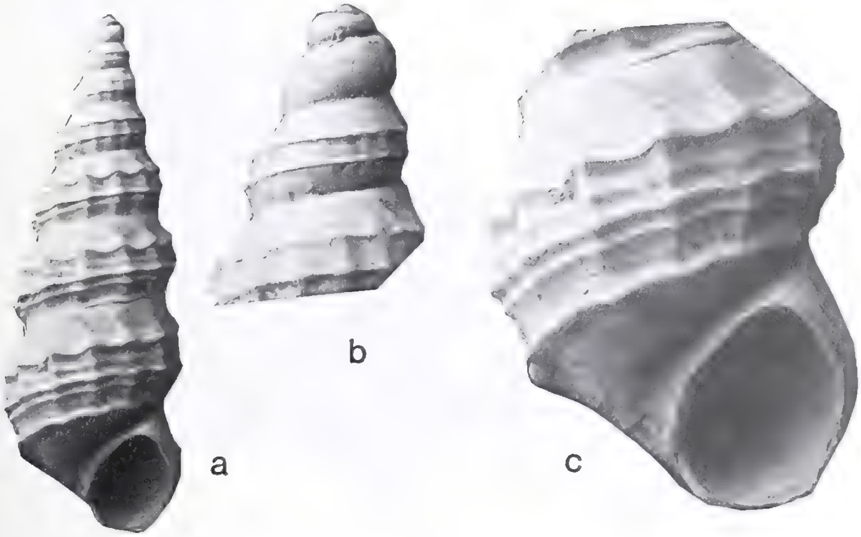
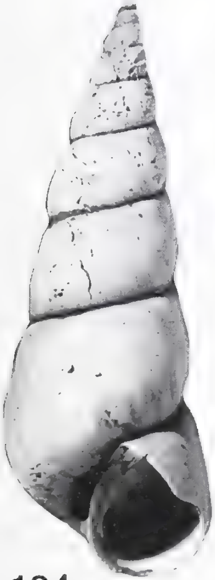


Fig. 103 *Dyris tuberculata* (de Greve). Pebasian; Iquitos, Peru. PIMUZ, unregistered. a, front, × 15; b, early spire whorls, × 50; c, body whorl and aperture, × 30.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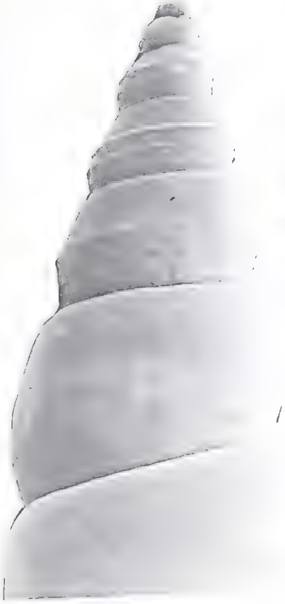
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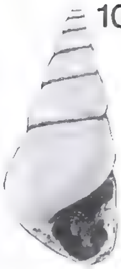
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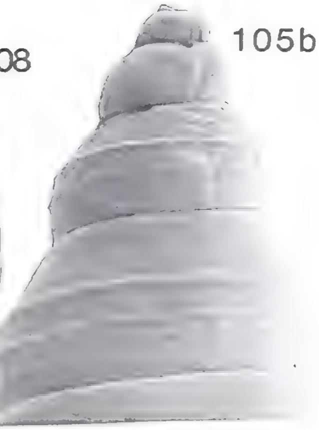
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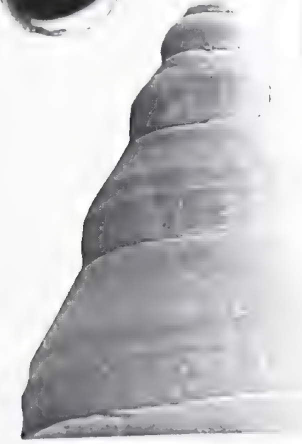
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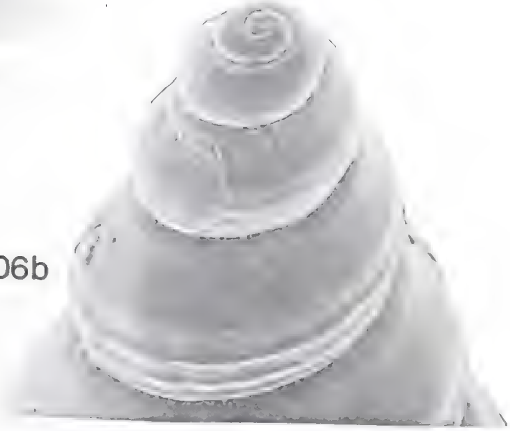
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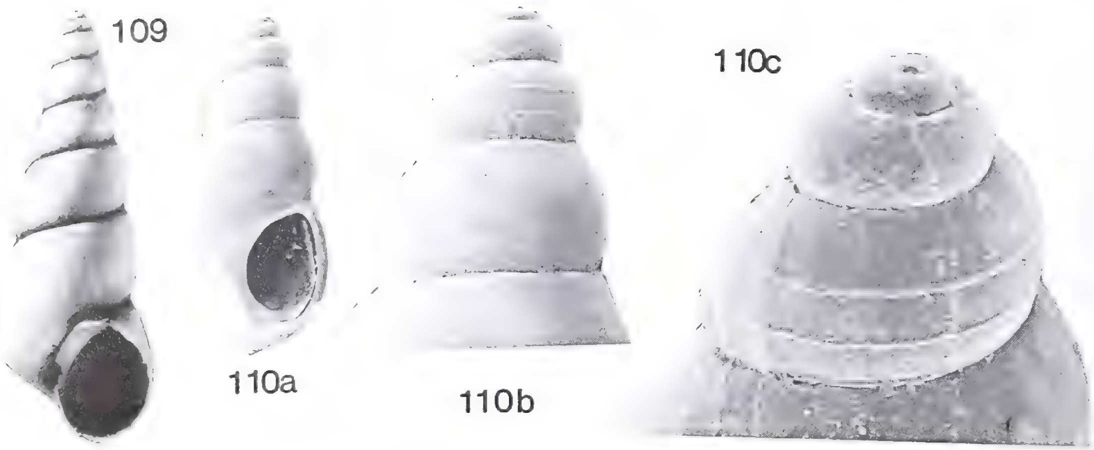
Figs 104–108 *Dyris ortoni* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. **104**, G25291; front, × 6. **105**, GG21632; a, × 15; b, × 30. **106**, GG21631; a, × 30; b, × 50. **107**, G25472, specimen figured by Woodward (1871: pl. 5, fig. 4) as *Odostomia* sp.; front, × 6. **108**, G25292; front, × 5.



Figs 109–110 *Dyris ortoni* (Conrad). Pebasian; Puerto Nariño, Colombia; Weeda Colln. **109**, GG19911; front, × 6. **110**, GG19912; a, front, × 10; b, early whorls, × 25; c, oblique view of apex, × 50.

Dyris ortoni (Gabb, 1869) Figs 104–112

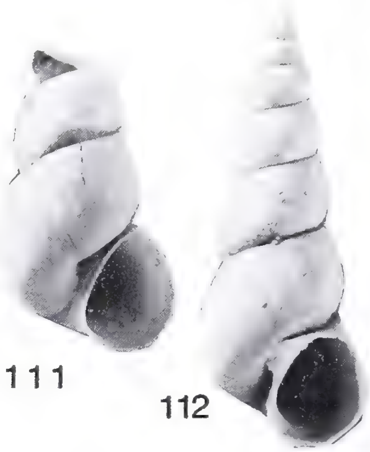
*. 1869 *Mesalia ortoni* Gabb: 198; pl. 16, fig. 3.
. 1871*b* *Isaea ortoni* (Gabb) Conrad: 193 (*pars*); pl. 10, fig. 13 (*non* pl. 10, fig. 10).
v. 1871 *Odostomia* ? Woodward: 103; pl. 5, figs 4a, b.
v. 1871 *Isaea (Mesalia) ortoni* (Gabb); Woodward: 108.
. 1878 *Hydrobia (Isaea) ortoni* (Gabb) Boettger: 490; pl. 13, figs 8a, b, 9a, b.
. 1878 *Hydrobia (Isaea) confusa* Boettger: 491; pl. 13, figs 4–7.
. 1924 *Isaea (Mesalia) ortoni* Gabb; Roxo: 49.
. 1926 *Hydrobia (Conradia) confusa* Boettger; Wenz: 1970.
. 1926 *Hydrobia (Conradia) ortoni* (Gabb); Wenz: 1971.
. 1938 *Hydrobia (Conradia) ortoni* (Gabb); de Greve: 79; pl. 1, figs 5, 6.
. 1938 *Hydrobia (Conradia) confusa* Boettger; de Greve: 80; pl. 1, figs 1–4.
. 1966 *Hydrobia confusa* Boettger; Willard: 65–68; pl. 63, figs 3, 4.
. 1966 *Isaea ortoni* (Gabb); Willard: 66–68, pl. 63, figs 1, 2.
. 1966 *Tryonia confusa* (Boettger) Taylor: 197.
. 1966 *Tryonia ortoni* (Gabb) Taylor: 197.
. 1969 *Dyris ortoni* (Gabb) Parodiz: 118.

TYPE MATERIAL. *Mesalia ortoni* Gabb (1869), described from Pebas, Peru. Presumed lost, as it is not listed as present in ANSP by Richards (1968).

Types of *Hydrobia confusa* Boettger (1878) not studied. Senckenburg Museum, Frankfurt (refigured by de Greve, 1938).

MATERIAL STUDIED. All Late Caenozoic. G25291–2, GG21631–4, GG21717–25, about 20 specimens, Pichana, Peru, Hauxwell Colln; GG19910–5, GG21726–35, about 60 specimens, Puerto Nariño, Colombia, Weeda Colln. G25472, Pichana, figured as *Odostomia*? by Woodward (1871), Hauxwell Colln.

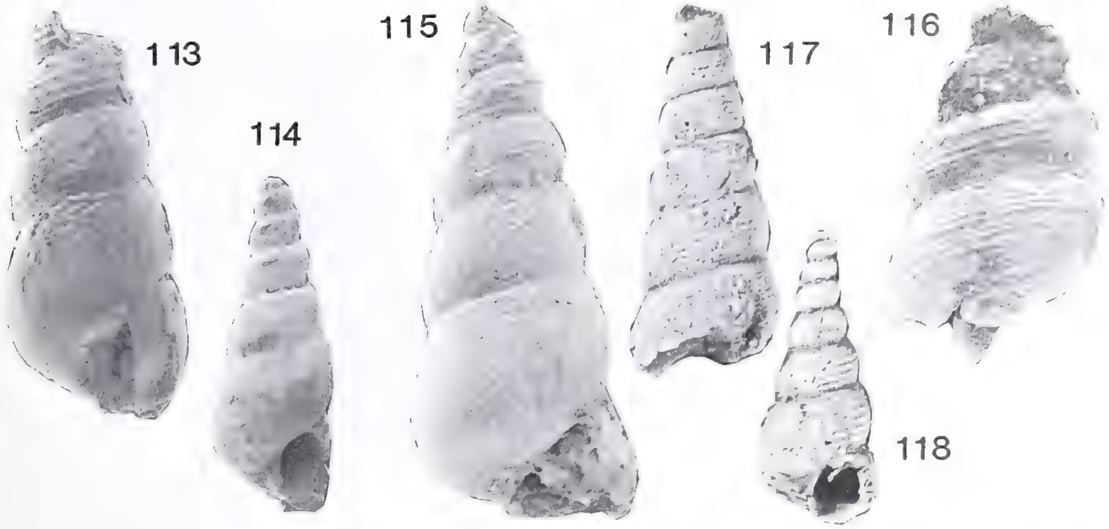
FURTHER OCCURRENCES. Late Caenozoic, Pebasian; Amazon Basin. Pebas (Gabb 1869, Boettger 1878); Três Unidos (Roxo 1924); Iquitos (de Greve 1938). Iquitos (Willard 1966: 65); Rio Marañon, 10 km above Iquitos (1966: 66); Rumi Tuni, 225 km north of Iquitos (1966: 67); 30 km north of Iquitos (1966: 68). No other records.



Figs 111–112 *Dyris ortoni* (Conrad). Pebasian; Puerto Nariño, Colombia; Weeda Colln. Both × 6. **111**, GG19913. **112**, GG19910.

DIAGNOSIS. Large, mainly smooth, high-spired *Dyris*, with spire angle between 15° and 33°, normally decreasing with growth; weak spiral sculpture usually confined to early whorls.

DESCRIPTION. The first two whorls are smooth, naticoid, and form a comparatively obtuse apex. The succeeding two or three whorls are also normally slightly less acute than the rest of the spire. Spiral sculpture is usually present and seldom consists of more than three randomly placed ribs which are normally confined to the third to fifth whorls. The uppermost rib forms an angulated shoulder, above which there is a broad, fairly steep, ramp. In most specimens, the rest of the shell is smooth except for clearly visible but weak growth lines. In a very small proportion of the shells from Puerto Nariño, up to about ten spiral ribs are present on all but a few of the earliest whorls. The whorl profile is broadly biconvex with the periphery well below half whorl height. The profile is often slightly flattened above the periphery and the maximum convexity occurs near the incised sutures. The aperture is fairly small, a third of shell height or less, tear-shaped, pointed above and rounded below. The inner lip is flared and



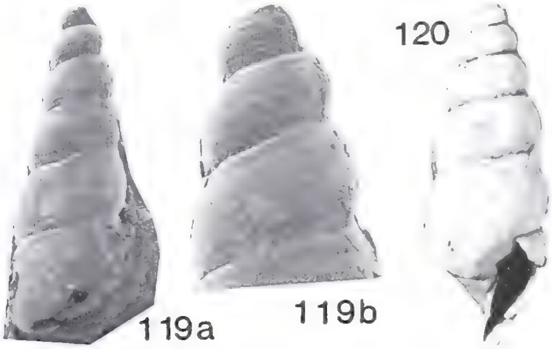
Figs 113–118 *Dyris* sp. Late Caenozoic; Loc. 33/480–560, La Tagua, Colombia; Eden Colln. **113**, GG19933/1; × 20. **114**, GG19933/2; × 20. **115**, GG19933/3; × 25. **116**, GG19933/4; × 15. **117**, GG19948/1; × 12. **118**, GG19948/2; × 12.

slightly detached from the base of the body whorl, exposing a small umbilicus.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Type of *Mesalia ortoni* Gabb; Pebas (from Gabb, 1869, h = 0.35").	8.9	–	–	–	24°
Lectotype of *Hydrobia confusa* Boettger; Pebas (from de Greve, 1938: pl. 1, fig. 1).	11.0	4.1	3.2	2.7	26°
Specimen figured by Boettger (1878) as *H. ortoni* (from de Greve, 1938: pl. 1, fig. 5).	9.8	3.3	2.2	4.5	20°
G25291, Pichana.	13.4	4.5	3.3	3.0	22°
G25292, Pichana.	6.7	2.9	2.2	2.3	32°
GG21631, Pichana.	9.5	3.6	–	–	–
G25472, *Odostomia*? of Woodward (1871)	5.7+	2.7	2.0	–	–
GG19910, Puerto Nariño.	9.5	3.4	2.6	2.8	22°
GG19911, Puerto Nariño.	7.6	2.8	2.4	2.7	22°
GG19912, Puerto Nariño.	4.7	2.2	–	–	32°

REMARKS. One of the specimens figured by Conrad (1871: pl. 10, fig. 13) is of this species but has not been seen and may be lost. The other (NYSM 9253) is of *Dyris tricarinata* (Boettger). The rich samples from both Pichana and Puerto Nariño suggest that *Hydrobia confusa* Boettger is merely a less aciculate form of *ortoni*, and, following Parodiz (1969), is placed in synonymy. The two forms nearly always occur together. De Greve (1938) records both *Hydrobia ortoni* and *H. confusa* from Iquitos and refigured Boettger's (1878) material from Pebas. The spire angles measured from de Greve's pl. 1 range from 15° to 19° for *H. ortoni* and between 28° and 33° for *H. confusa*: not between 30° 30′ and 39° 30′ as given in his text. The most acutely spired example of *H. ortoni* that de Greve figured (1938: pl. 1, fig. 6) has a markedly obtuse apex.

D. ortonii may be recognized by its large size and comparative smoothness. The spirally sculptured early whorls distinguish it from the smooth-shelled living *Heleobia* and *Littoridina*, whilst living *Lyrodes* has weaker but more persistent spiral sculpture covering a much greater proportion of the shell surface.



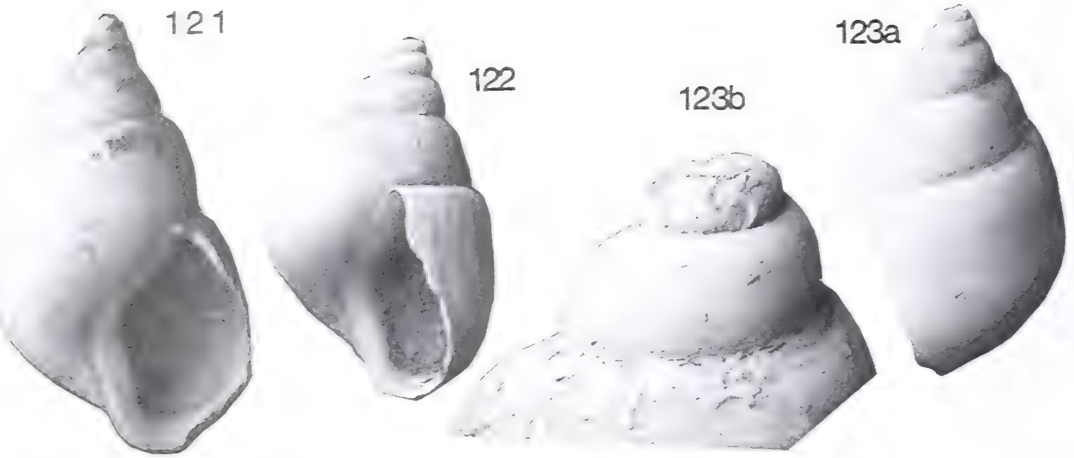
Figs 119–120 *Dyris* sp. Late Caenozoic; La Tagua, Colombia; Eden Colln. **119**, Loc. 33/560, GG 19932/1; a, × 10; b, early whorls to show spiral ribbing, × 25. **120**, Loc. 54, GG19949; × 15.

Dyris sp. Figs 113–120

v. 1982 *Dyris gracilis* Conrad; Nuttall *in* Bristow & Parodiz: 20.
v. 1982 *Hydrobia* cf. *ortoni* (Gabb); Nuttall *in* Bristow & Parodiz: 20.

MATERIAL STUDIED. All Late Caenozoic, La Tagua (Eden Colln). GG19932/1–2, Loc. 33, 560 cm; GG19933–4, GG19935/1–6, GG19948/1–5, Loc. 33, 480–560 cm; GG19949/1–3, Loc. 54.

REMARKS. The material is too poorly preserved and fragmentary to justify formal description. The above samples consist of small aciculate gastropods, with fine spiral sculpture: some specimens are virtually smooth, but this is probably the result of wear. It is not entirely certain that only one species is present (see above synonymy). Nuttall *in* Bristow & Parodiz (1982) referred the spirally-ribbed specimens to *D. gracilis* and the smooth shells to *Hydrobia* cf. *ortoni*. These determinations were made before type and other well documented



Figs 121–123 *Littoridina crassa* (Etheridge). Pebasian; Canamá, Peru; Barrington Brown Colln. **121**, GG19993/1, lectotype, figured by Etheridge (1879: pl. 7, fig. 11) as *Hydrobia dubia* Etheridge, and by Kadolsky (1980: figs 13, 14) as *Littoridina crassa*; front, × 10. **122**, paralectotype, GG19993/2; between front and side view, × 10, to show columella and outer lip. **123**, paralectotype, GG19993/3; a, side, × 10; b, apical whorls from side, × 30.

material could be examined. By extrapolation from broken fragments, the height would appear to be about 5 mm and the breadth 1.6 mm. The apex is blunt, but the spire angle averages only about 20°. About six spiral threads may be counted with difficulty, and their spacing is variable. In some specimens they occur over the whole surface of each whorl, but in others they are closely spaced and confined to below the periphery.

These specimens cannot be matched with any described species, though they have some resemblance to juvenile shells of *D. lintea*, which, however, are considerably less aciculate.

Genus ***LITTORIDINA*** Souleyet, 1852

?Littoridina crassa (Etheridge, 1879) Figs 121–123

*v 1879 *Assiminea crassa* Etheridge: 86.
* 1879 *Hydrobia dubia* Etheridge: 86; pl. 7, fig. 11.
v. 1980 *Littoridina crassa* (Etheridge) Kadolsky: 371, figs 13, 14.
v. 1982 *Toxosoma eboreum* Conrad; Parodiz *in* Bristow & Parodiz: 41 (*pars*, *non* fig. 16).

LECTOTYPE of *Assiminea crassa* Etheridge, GG19833/1 (*ex* BMPD 97225), Late Caenozoic, Pebasian; Canamá (C. Barrington Brown Colln), selected by Kadolsky, 1980: 371, fig. 13. GG19833/2, 3, information as above, are paralectotypes. The type specimens of *Hydrobia dubia* Etheridge, 1879, are presumed either lost or mixed by mistake with the type specimens of *A. crassa* from the same locality, horizon and collection. One was figured by Etheridge (1879: pl. 7, fig. 11) and copied by Kadolsky (1980: fig. 14). No further occurrences known.

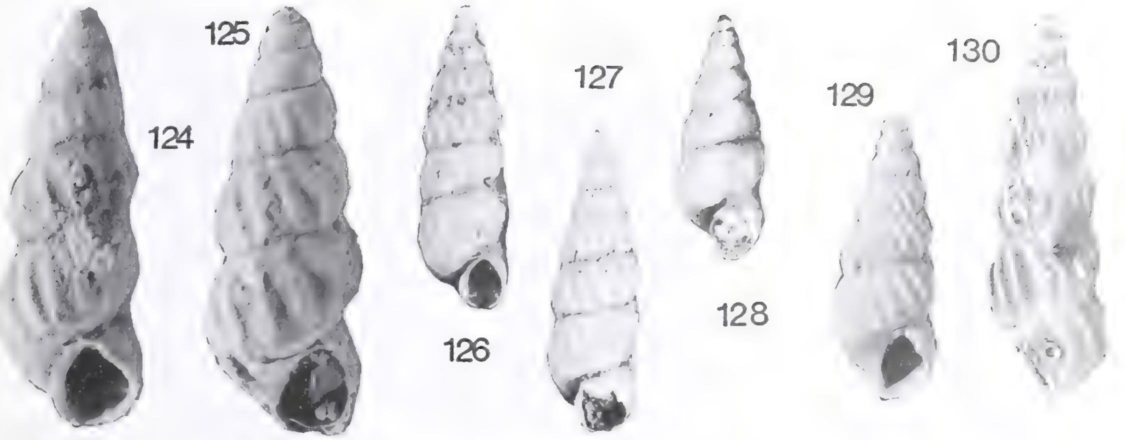
DIMENSIONS. In mm.	h	br	hap	h/br	sa
GG19833/1, Canamá.	5.9	3.7	2.5	1.59	55°
GG19833/2, Canamá.	4.9	3.1	2.3	1.56	–
GG19833/3, Canamá.	4.6	3.0	2.2	1.53	–

REMARKS. The three specimens BMPD 97225 were labelled as '*Assiminea crassa* Etheridge' by L. R. Cox, but in common with the other surviving specimens in Barrington Brown's collection from Canamá, there is no earlier label. In view of the obvious similarity between the specimens labelled *A. crassa* and Etheridge's type illustration of *H. dubia*, I concur with Kadolsky's decision to synonymize the two. Parodiz *in* Bristow & Parodiz (1982) placed *Hydrobia (Paludestrina) dubia* Etheridge in the synonymy of *Toxosoma eborea* Conrad, and thought that Etheridge's species resembled in particular specimens from Iquitos, figured by de Greve (1938: pl. 5, figs 24, 29, 33, 34) as *Pseudolacuna macroptera* Boettger. *Toxosoma eborea* has a columellar fold, whereas the present species does not. There is no basis for the synonymy suggested by Parodiz and there is no doubt that de Greve's specimens all belong to *T. eborea*.

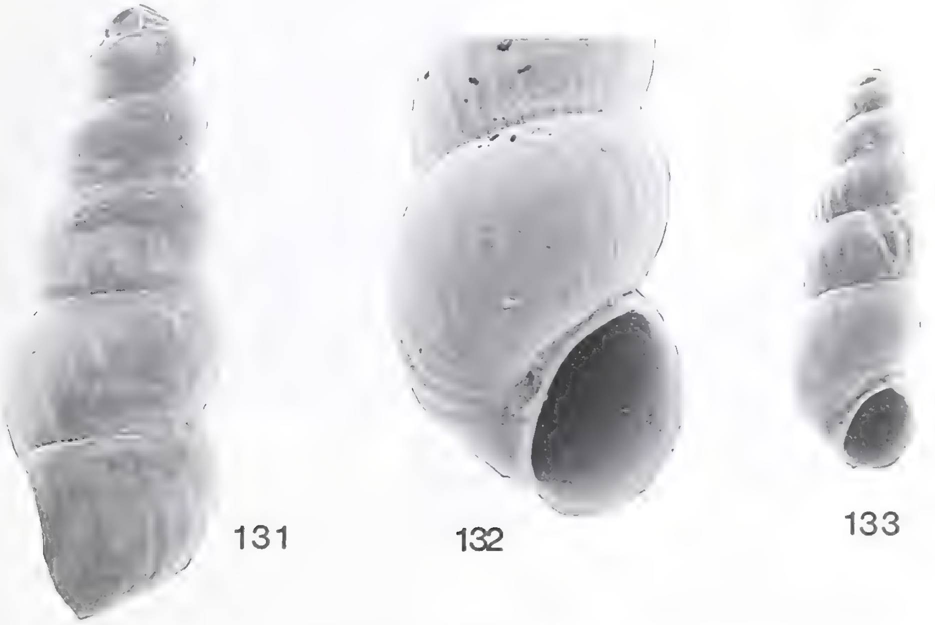
This species cannot be placed in any described genus with complete confidence. Following Kadolsky, who also expressed reservations on this point, it is very tentatively assigned to *Littoridina*. It may be distinguished from comparatively smooth species of *Dyris* such as *D. ortoni* Conrad by its complete lack of sculpture, apart from slightly sinuous but basically orthocline growth lines. In addition, its inner lip is not rimmed: it is more strongly calloused than that of *Dyris, Liris* and *Heleobia* but not as strongly as in either *Eubora* or *Potamolithus*. An important feature is the shape of this lip. In all the above-mentioned genera, the inner lip forms a fairly uniform curve whose centre lies well to the right of the columella. In '*L.' crassa*, on the other hand, the lower part of this lip, formed by the columella, is straight and leans slightly to the right, whilst the upper, parietal region, bulges strongly to the right. The outer lip is damaged in all three specimens: growth lines suggest, however, that no more than an extremely weak broad sinus is situated just to the right of the base of the columella. A posterior notch is present.

Genus ***LIRIS*** Conrad, 1871

TYPE SPECIES. *Liris laqueata* Conrad, 1871*b*, Late Caenozoic, Pebasian; Pichana, Peru (= *Turbonilla minuscula* Gabb, 1869, Pebas). By monotypy.



Figs 124–130 *Liris minuscula* (Gabb). Pebasian. **124–125**, Pebas, Peru; Orton Colln. **124**, ANSP 31397a, **lectotype** (of *Turbonilla minuscula* Gabb), here selected; front, × 15. **125**, ANSP 31397b, accompanying paralectotype; front, × 15. **126–130**, Pichana, Peru; Hauxwell Colln. **126**, NYSM 9259a, **lectotype** of *Liris laqueata* Conrad, here selected; front, × 10. **127**, NYSM 9259b, accompanying paralectotype; front, × 10. **128**, NYSM 9259c, accompanying paralectotype; front, × 10. **129**, GG21641; front, × 15. **130**, GG19969; side, × 25.



Figs 131–133 *Liris minuscula* (Gabb). Pebasian; Pichana, Peru; Hauxwell Colln. **131**, GG21640; side, × 40. **132**, GG21642; body whorl and aperture, × 50. **133**, GG19965; front, × 25.

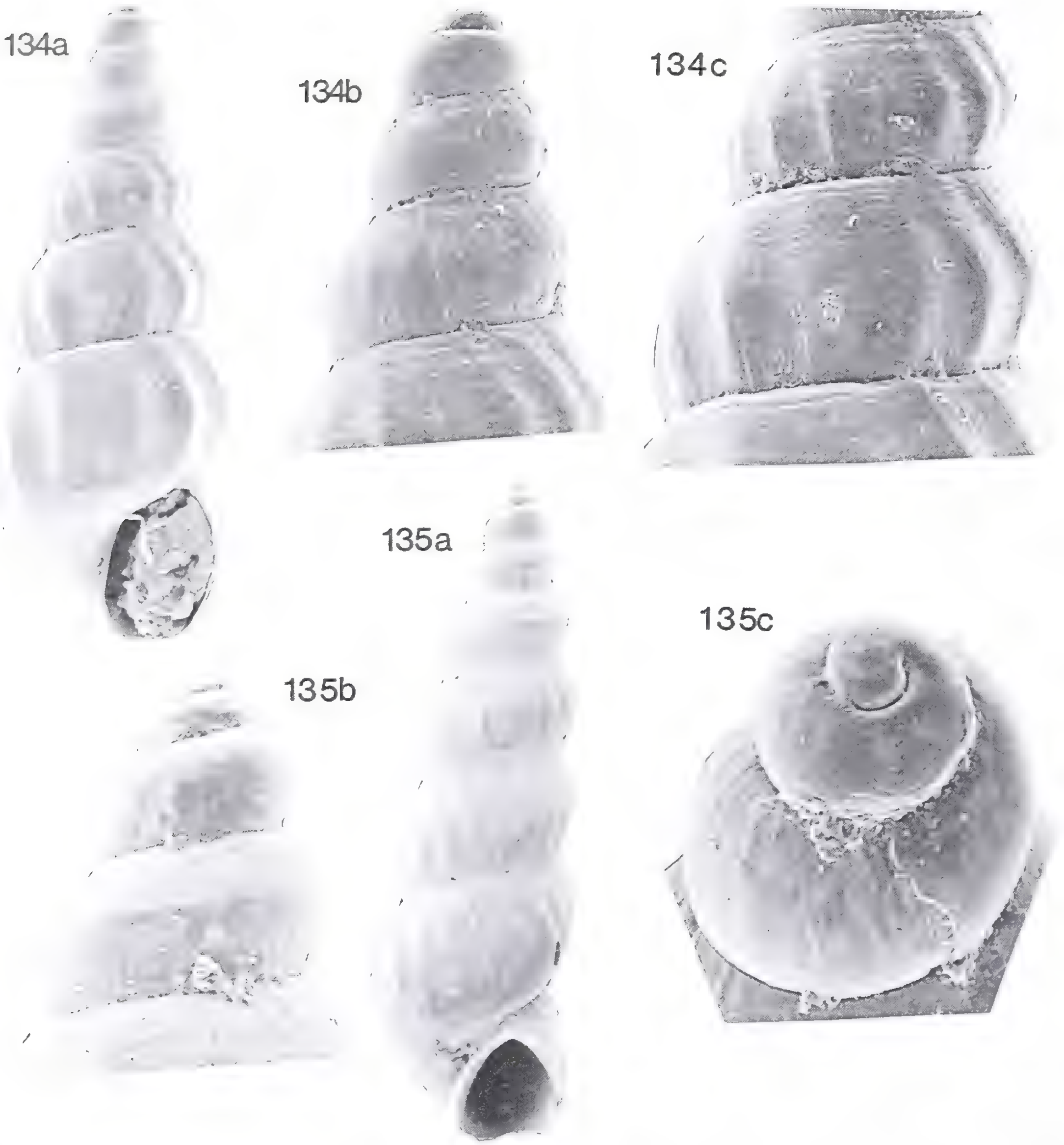
Diagnosis. Littoridinid with *c.* 12–18 axial, apparently not quite collabral, folds per whorl; growth lines prosocline; spiral sculpture absent or weak, often confined to early whorls.

Other species assigned. Late Caenozoic, Pebasian: *Liris acicularis* sp. nov., Pichana, Peru; *Melania scalarioides* Etheridge, 1879, Canamá; ?Miocene, Tumbatú Formation, Chota Basin, Ecuador; *Liris* sp. (p. 208)

Generic distribution. Late Caenozoic, Pebasian; Upper Amazon Basin. Pebas (Gabb 1869, Boettger 1878, Willard 1966); Pichana (Conrad 1871*b*); Iquitos (de Greve 1938, Willard 1966); ?Cachoera das Tracoas, Brazil (Roxo 1924); Três Unidos, Peru (Roxo 1924, Costa 1980); Puerto Nariño, Colombia. ? Miocene, Chota Basin, Ecuador. Unknown living.

Remarks. *Liris* resembles the living North American genus *Tryonia* (type species, *T. clathrata* Stimpson, 1865*b*). However, the latter has a more obtuse spire, and its folds are noticeably noded at the periphery and are truly collabral. Furthermore, its outer lip is bent forward adapically, whilst in *Liris* the reverse is true, with the growth lines disposed at a greater angle from the vertical than the folds. The aperture of *Tryonia* is relatively larger than that of *Liris*.

Comparison of the originally poorly illustrated type specimens of *Turbonilla minuscula* Gabb and of *Liris laqueata* Conrad with BMPD material from Pichana show that the two are synonymous, as was first suspected by Boettger (1878). On the other hand, de Greve (1938) was correct in recognizing that two quite similar species occurred together at Iquitos. All those that he figured as *L. minuscula* are now however referred to *L. scalarioides* (Etheridge) and those that he



Figs 134–135 *Liris minuscula* (Gabb). Pebasian; Pichana, Peru; Hauxwell Colln. **134**, GG19964; a, front, × 40; b, early whorls, × 90; c, middle whorls, × 75. **135**, GG19967; a, front, × 40; b, early whorls, × 115; c, oblique view of apex, × 190.

figured as *L. laqueata* are here placed in *L. minuscula*. Similarly, the distinctions given by Parodiz (1969: 119, 120) between *L. minuscula* and *L. laqueata* apply respectively to *L. scalarioides* and *L. minuscula* instead. These reidentifications also result in the locality data for the various species given by Taylor (1966: 197) being sometimes incorrect.

The unfigured references of Willard (1966) can, in view of the confusion over specific determinations, be treated only as evidence for the presence of the genus at his localities. Thus, the authenticated distribution of this genus is very restricted. It appears, unlike *Dyris*, to be almost entirely confined to the 'classic' Pebasian localities of the Upper Amazon Basin. The one exception so far known is the record from the Tumbatú Formation of Ecuador.

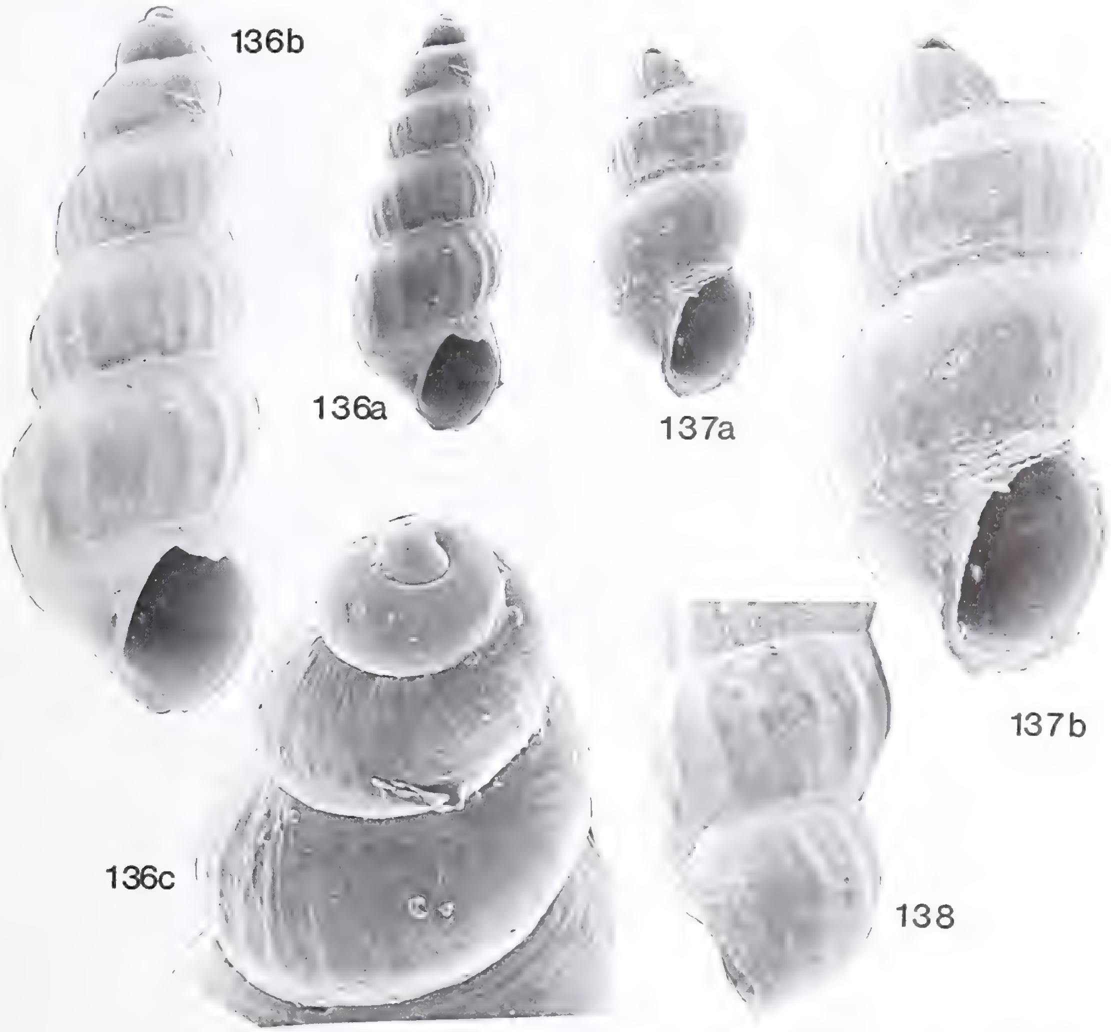
Liris minuscula (Gabb, 1869) Figs 124–138

*v 1869 *Turbonilla minuscula* Gabb: 197; pl. 16, fig. 1.
v. 1871*b* *Liris laqueata* Conrad: 194; pl. 10, fig. 3; pl. 11, fig. 8.
. 1878 *Turbonilla minuscula* Gabb; Boettger: 496; pl. 13, fig. 13.
. 1938 *Liris laqueata* Conrad; de Greve: 89; pl. 2, figs 10, 14–31; text-figs 6–11.
1966 *Tryonia laqueata* (Conrad) Taylor: 197 (*pars*).
1966 *Tryonia minuscula* (Gabb) Taylor: 197 (*pars*).
1969 *Liris laqueata* Conrad; Parodiz: 120.

LECTOTYPE of *Turbonilla minuscula* Gabb, 1869, ANSP 31397a, here selected. Late Caenozoic, Pebasian; Pebas, Peru (Orton Colln). ANSP 31397b (same information) is a paralectotype.

Lectotype of *Liris laqueata* Conrad, 1871, one of NYSM 9259, original of Fig. 126 herein, here selected. Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln). Two other specimens registered under NYSM 9259 (same information), Figs 127–8, are paralectotypes.

OTHER MATERIAL STUDIED. G25288/1–4, Pichana, as above (Hauxwell Colln); GG19964–70, GG21639–49, Pichana (Hauxwell Colln, extracted from matrix 1982).



Figs 136–138 *Liris minuscula* (Gabb). Pebasian; Pichana, Peru; Hauxwell Colln. **136**, GG19966; a, front, × 40; b, same, × 66; c, oblique view of apex, × 150. **137**, GG21639; a, front, × 40; b, same, × 75. **138**, GG19968; side, × 40.

FURTHER OCCURRENCES. Late Caenozoic, Pebasian; Pebas (Boettger 1878), Iquitos (de Greve 1938). No other records.

DIAGNOSIS. *Liris* with low, well-rounded, sometimes obsolescent, axial folds; spiral sculpture mainly of very weak spiral threads; spire angle between 15° and 27°.

DESCRIPTION. The rather high, naticoid, apex is smooth and consists of 2–2½ whorls. Although rare individuals, including one of the paralectotypes of *L. laqueata* Conrad, lack axial folding, in most shells axial folding appears on the third whorl. The folds are slightly noded at the periphery for the next four whorls or so in a minority of specimens. The number of folds varies 12–16 per whorl and their strength also varies, not only from specimen to specimen, but also in any one individual: in some cases they may be virtually obsolete. The folds die away at the lower suture and are absent from the lower half of the body whorl. Spiral sculpture is visible only on exceptionally well-preserved individuals. It consists of extremely weak threads situated mainly, but not exclusively, on the upper half of the whorl. A weak carination, forming a shoulder, is rarely present. Another carination at the lower suture is seen in the majority of specimens. Weak spiral threads are also found on the neck of the body whorl. The spire angle varies considerably and is not constant in individuals, decreasing with growth to give a slightly pupiform appearance. The aperture is constricted, normally being under half the height of the last whorl. The peristome is markedly detached in some of the Iquitos shells figured by de Greve (1938), but is only slightly so in the specimens studied herein from both Pebas and Pichana.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
ANSP 31397a, lectotype of *Turbonilla minuscula*, Pebas.	3.7	1.4	0.8	2.8	22°
ANSP 31397b, paralectotype as above.	3.8	1.3	–	2.9	–
NYSM 9259a, lectotype of *Liris laqueata* Conrad, Pichana.	4.1	1.2	0.7	3.4	15°
GG19967, Pichana.	2.5	0.75	0.6c	3.3	18°
GG19964, Pichana.	2.15	0.8	0.4	2.7	27°
GG19965, Pichana.	1.9	0.6	0.4	3.2	15°
GG19966, Pichana.	1.4	0.5	0.3	2.8	15°

REMARKS. Examination of the type material of *L. minuscula* and *L. laqueata* leaves no doubt that the two are conspecific.

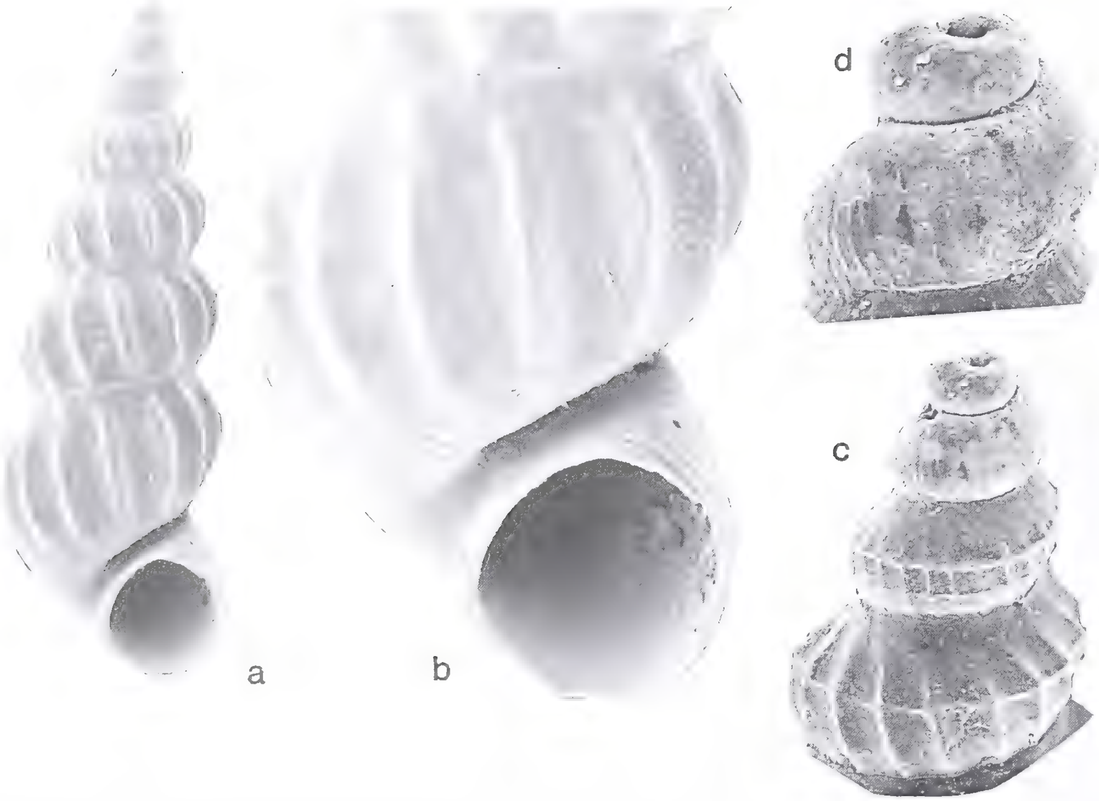


Fig. 139 *Liris scalarioides* (Etheridge). Pebasian; Puerto Nariño, Colombia; Weeda Colln. GG21560; a, front, × 20; b, body whorl and aperture, × 50; c, oblique view of early spire whorls, × 50; d, oblique view of apex, × 100. See also Fig. 456, p. 354.

Several records of these species are now included under *L. scalarioides* (Etheridge) (below), where comparisons between the two species are given.

Liris scalarioides (Etheridge, 1879) Figs 139–146, 456

*v 1879 *Melania scalarioides* Etheridge: 88; pl. 7, fig. 8.

. 1924 *Melania scalarioides* Etheridge; Roxo: 48.

. 1938 *Liris minuscula* (Gabb); de Greve: 92; pl. 1, figs 31–35; pl. 2, figs 1–9, 11–13; text-figs 12–18.

? 1966 *Tryonia minuscula* (Gabb); Taylor: 197 (*pars*).

. 1969 *Liris minuscula* (Gabb); Parodiz: 120.

. 1980 *Liris minuscula* (Gabb); Costa: 881; pl. 2, figs 1–4.

. 1981 *Liris minuscula* (Gabb); Costa: 643; pl. 1, figs 9, 10.

LECTOTYPE. GG22419, selected herein, the specimen figured by Etheridge, and the accompanying paralectotype GG22420 (both *ex* 97724); Late Caenozoic, Pebasian; Canamá, Peru; Barrington Brown Colln.

OTHER MATERIAL STUDIED. GG19852, GG19986–90, and GG21560–9 (over twenty shells), from Puerto Nariño, Colombia; Weeda Colln.

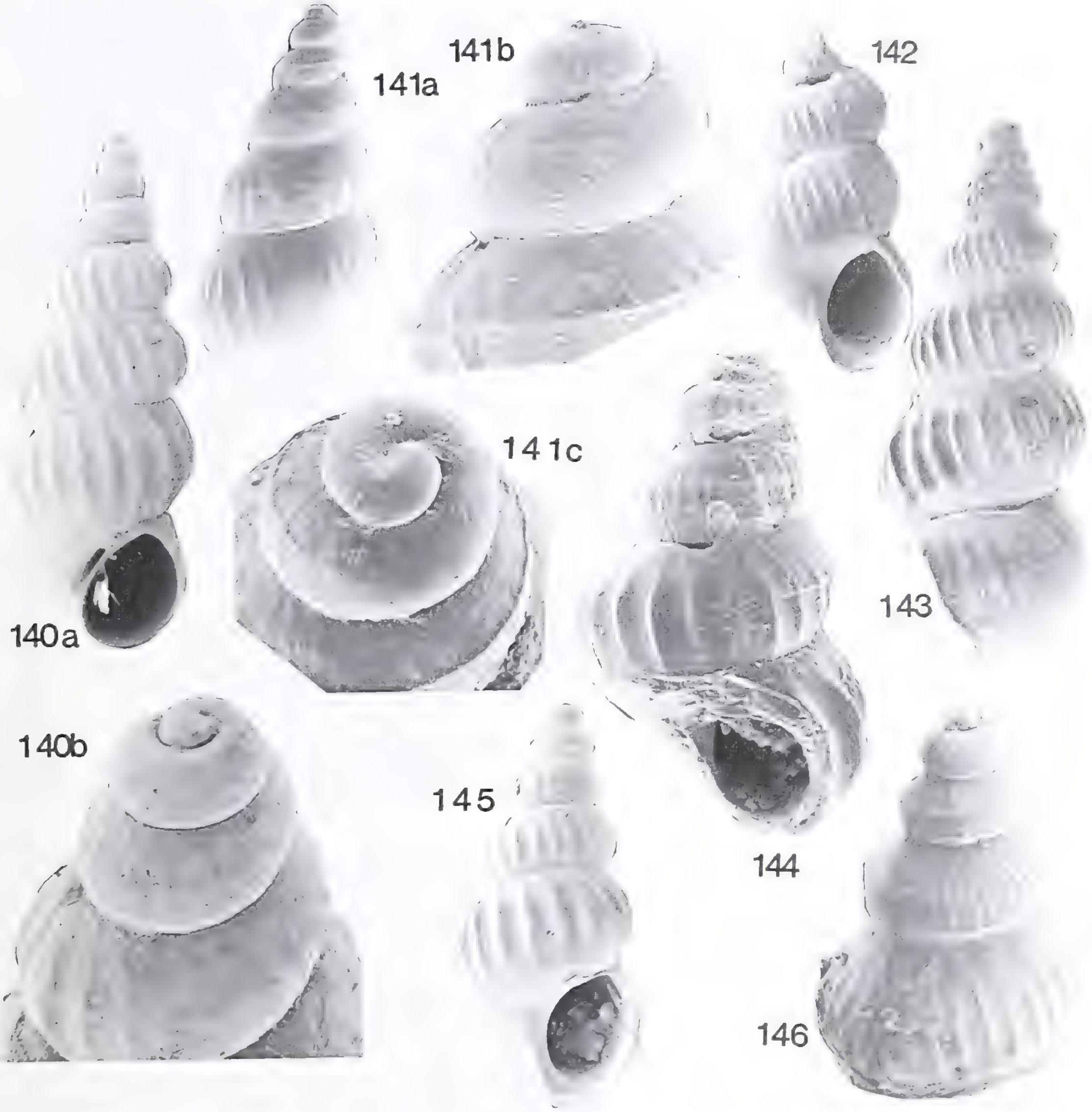
FURTHER OCCURRENCES. Late Caenozoic, Pebasian; Iquitos, Peru (de Greve 1938); ?Cachoero das Tracoas, Brazil (Roxo 1924); Três Unidos, Peru (Roxo 1924, Costa 1981); Afloramento em Atalaia do Norte and CPCAN III, Sao Paulo de Olivença, Brazil (Costa 1980).

DIAGNOSIS. Large *Liris* with two or three carinate post-apical whorls; 14–25 sharply crested axial folds per whorl; spire angle 22°–32°.

DESCRIPTION. The apex is much larger than that of *L. minuscula*. The first whorl is disjunct and the second biconvex. Variation is shown in the development of the next three whorls or so. Usually a carina appears at mid whorl-height, with a straight, sloping, ramp above and a convex whorl side below. Below the carina, there are sometimes traces of weak spiral ribbing and also another carination coinciding with, and sometimes obscured by, the suture. All traces of spiral sculpture are lost thereafter for the remaining three to five whorls. The axial sculpture appears at the same time as the carina. At first, it is virtually confined to the lower half of the whorl and is sharply truncated by the sutural carina. There are 14–25 axial ribs per whorl, whose strength varies considerably, but all have narrow, slightly rounded crests, separated by wide concave interspaces. On the later spire whorls, some ribs stretch from suture to suture, but others do not touch the adapical suture. Ribs decrease in strength below the periphery and are absent, not only from the base of, but also often from the latter part of, the body

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Lectotype GG22419.	4.1+	1.8	1.0	2.3	30°
GG21560.	4.4	1.4	0.7	3.1	22°
GG21561.	4.7	1.6	1.0	2.9	27°
GG21562.	2.7	1.1	0.8	2.5	32°
GG21563.	3.8	1.3	–	2.9	27°

All specimens from Puerto Nariño, except the lectotype (from Canamá). Greatest height for Iquitos specimens given by de Greve (1938: 95) was 6.0 mm.



Figs 140–146 *Liris scalarioides* (Etheridge). Pebasian; Puerto Nariño, Colombia; Weeda Colln. **140**, GG21561; a, front, × 15; b, oblique view of apex, × 50. **141**, GG21565; a, rear, × 20; b, oblique view of apex, × 50. **142**, GG19986; front, × 20. **143**, GG21563; side, × 20. **144**, GG21566; showing sculpture of early whorls, × 50. **145**, GG21562; front, × 20. **146**, GG21567; oblique view of early whorls, × 40. See also Fig. 456.

whorl approaching the aperture. The aperture is slightly constricted. In both Puerto Nariño and Iquitos shells, the peristome is sometimes detached.

REMARKS. The best specimens studied are those from Puerto Nariño. The lectotype is rather worn, and the paralectotype is incomplete. The diagnosis is sufficient to separate this species from *L. minuscula*. Costa's illustrations (particularly 1980: pl. 1, figs 1, 2), which show the carina typical of the young stages of *L. scalarioides*, confirm that not only her own records, but also that of Roxo (1924), should fall into the above synonymy. Further support for this redetermination is afforded by Costa's synonymy, which included references to the good figures quoted above of *L. minuscula* de Greve (1938), *non* Gabb, rather than de Greve's figures of '*L. laqueata*' which are, in fact, of *L. minuscula*: see p. 204.

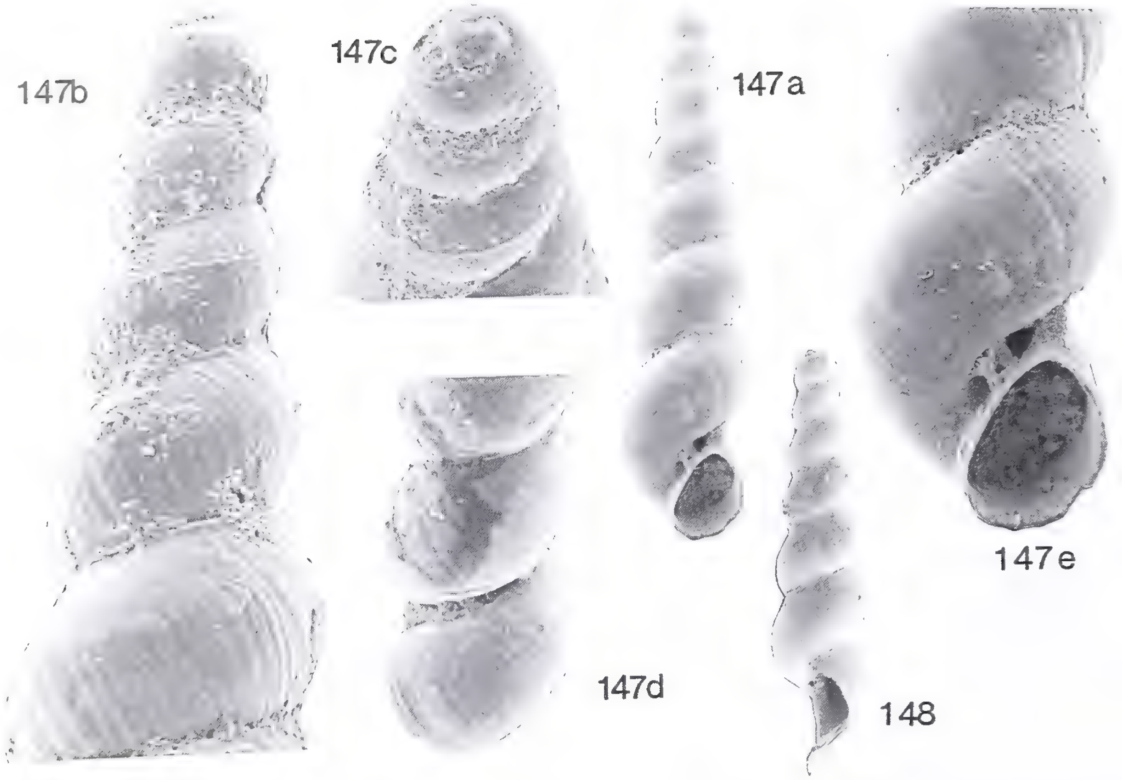
Liris acicularis sp. nov. Figs 147–148

HOLOTYPE. GG21666, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln, extracted 1982). GG21667–9, same details as holotype, are paratypes.

NAME. 'Sharply pointed'.

DIAGNOSIS. Pointed, straight-sided *Liris* with spire angle of about 11°; shell sculptured with extremely weak spiral threads, and weak carinae situated at periphery and lower suture; growth lines comparatively strong in relation to spiral threads.

DESCRIPTION. The first whorl is very small in relation to the bulbous second whorl. Subsequent whorls are distinctly less convex: their periphery is at mid-height and marked by a weak carina. A second carina occurs at, or just above, the



Figs 147–148 *Liris acicularis* sp. nov. Pebasian; Pichana, Peru; Hauxwell Colln. **147**, **holotype**, GG21666; a, front, × 30; b, early spire whorls, × 90; c, oblique view of apex, × 90; d, rear view of last whorls, × 50; e, body whorl and aperture, × 60. **148**, paratype, GG21667; × 30.

lower suture. Weak spiral threads are visible at magnifications of about × 30. The growth lines, in contrast, are comparatively strong; they are both opisthocline and prosocline, sloping backwards from the adapical suture. The peristome is markedly detached in the holotype, but less so in those paratypes in which the mouth is not damaged. The spire is virtually straight-sided from the second whorl to the ninth or body whorl.

DIMENSIONS. In mm.	h	br	hap	sa
Holotype, GG21666.	2.3	0.6	0.33	11°
Paratype, GG21667.	1.9	0.4	–	10°

REMARKS. These few specimens are described as a new species, which is assigned to *Liris* with some reservations. They do not appear to grade into *L. minuscula* (Gabb). They are noticeably sharply pointed, and are characterized by their very straight-sided spires, whilst both *L. minuscula* and *L. scalarioides* are definitely slightly pupiform. Rare specimens of *L. minuscula*, including one of the paratypes of *L. laqueata* Conrad and GG21460 (both also from Pichana) lack axial folding. However, they are much stouter shells and their growth lines are not strongly prosocline.

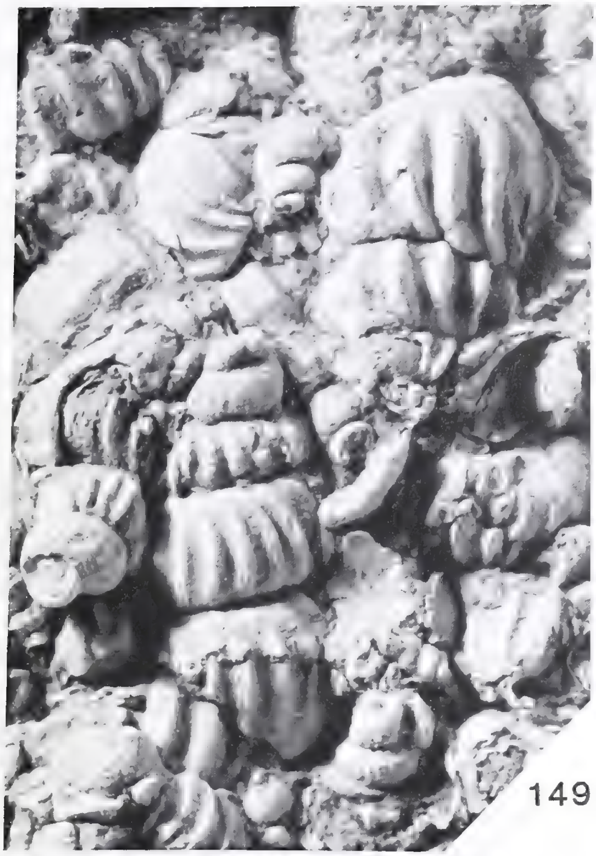
Dyris gracilis Conrad possesses a variable number of carinae: one shell from Pichana has only one carina, which, being situated at the periphery, corresponds with the weak carina of *L. acicularis*. The apertural features of the present species, in particular the detached peristome, are more reminiscent of *Liris* than *Dyris*, and consequently it is assigned to the former. Nevertheless, there must remain some doubt not only about its generic placing, but also the criteria used for separating the two genera.

Liris sp. Figs 149–153

v. 1977 *Potamides* n. sp.; Bristow & Hoffstetter: 337.
v. 1982 *Liris* aff. *minuscula* (Gabb); Bristow & Parodiz: 5.
v. 1982 *Liris minuscula* (Gabb); Bristow & Parodiz: 6, 40.

MATERIAL STUDIED. Middle Tumbatú Formation, Chota Basin, Ecuador. GG19807/1–10, Loc. PH 1, 0° 29′ N, 78° 03′ W; GG19808/1–10, Loc. PH 2, 0° 28′ N, 78° 03′ W. No further occurrences.

REMARKS. The material consists of thin – up to 20 mm thick – blocks of a buff-coloured shell conglomerate crowded with apparently unorientated and broken specimens. Bristow & Parodiz (1982: 5) refer to thin shell beds (10 to 20 cm thick) in the middle unit of the Tumbatú Formation. It is not known whether PH 1 and PH 2, which are very similar in appearance, represent both or only one of these beds. Bristow & Parodiz state (1982: 40) that some of the material they examined came from the San Cayetano Formation (? Upper Miocene) of the Loja Basin, Ecuador. They do not mention this species in the discussion of the fauna, flora and age of this formation (1982: 16), but do refer to *Dyris* cf. *gracilis* Conrad 'form' *tricarinata* (Boettger) occurring in BMPD samples (JW 424; Carrion Colln). The presence of *D. tricarinata* in the San Cayetano Formation is provisionally accepted herein. This material consists of well-bedded marl with internal moulds encrusted by some artefact rather resembling mud cracks. These could have been confused with the axial ribbing of *Liris*. No specimens referable to *Liris* from the San Cayetano Formation can be traced in BMPD.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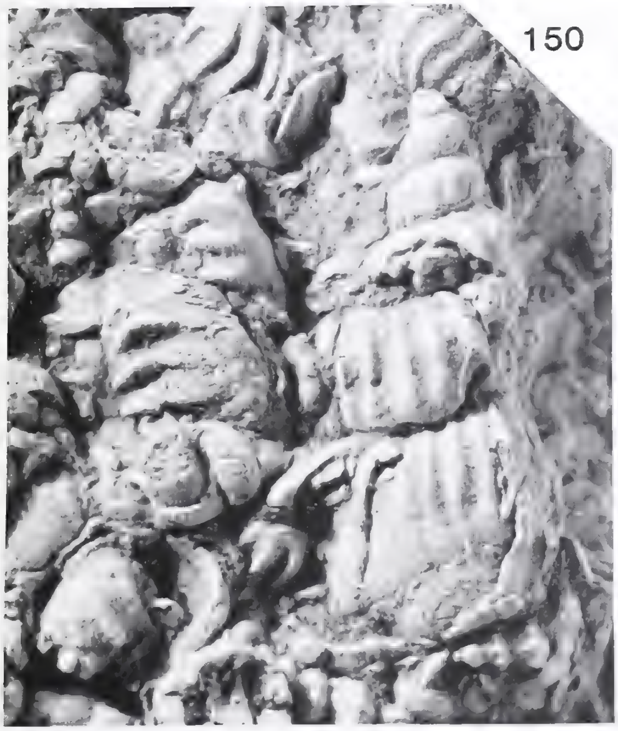
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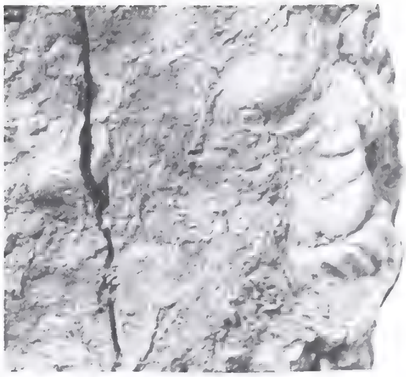
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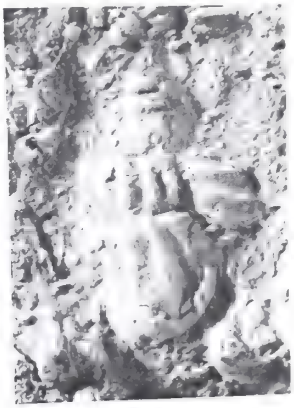
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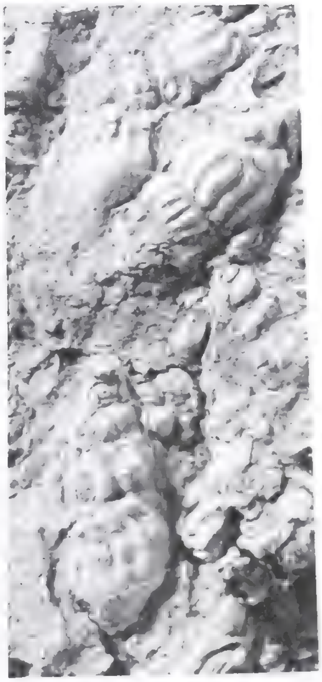
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Figs 149–153 *Liris* sp. Neogene, Middle Tumbatu formation; Chota Basin, Ecuador; C. R. Bristow Colln. **149–150** both × 8, Loc. PH 2. **149**, GG19808/2. **150**, GG19808/1. **151–153** all × 5, Loc. PH 1. **151**, GG19807/1. **152**, GG19807/2. **153**, GG19807/3.

The specimens in samples PH 1 and PH 2 are rather large for *Liris*: it is estimated that, if undamaged, many would have exceeded 10 mm in height. Frequent fracture marks show that many specimens are crushed. It is impossible to determine whether one or two species are present because of the variation in sculpture, not only on individual shells, but also between different specimens. All have strong axial folding: it is not possible to see whether the growth lines are truly parallel to the folds. Some whorls appear to lack all traces of spiral sculpture, others show weak spiral threads, whilst the remainder possess, in addition, a distinct but weak carinate shoulder. Some specimens appear to have early post-nuclear whorls which are much higher than broad: these are very unlike those of described species of *Liris*, at least at specific level. The rounded apertures and strong axial sculpture suggest, however, that many of them belong to a species with some resemblance to *Liris scalarioides* (Etheridge), which is, however, distinctly smaller. They clearly do not belong to *L. minuscula* (Gabb).

The only fossils known from the Tumbatú Formation, other than the present material, are plant fragments (Bristow & Parodiz 1982: 5, 6). The presence of *Liris* suggests some correlation with the Pebasian of the Upper Amazon Basin, and hence a probable Late Caenozoic age.

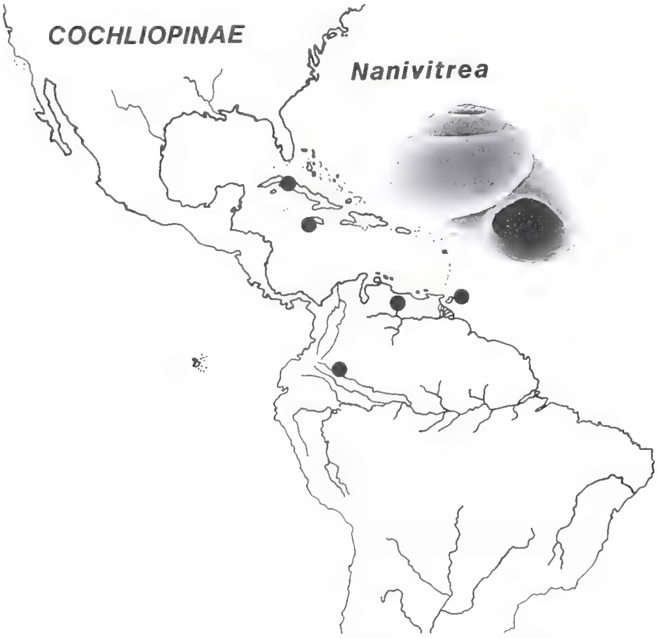


Fig. 154 Neogene and Recent distribution of Cochlopinae. ●, *Nanivitrea*; all records are Recent except those from La Tagua. Inset, *Nanivitrea colombiana* sp. nov.; La Tagua, Colombia.

Subfamily **COCHLIOPINAE** Tryon, 1866

[Tryon, 1866*a*, emended Taylor, 1966]

Taylor (1966: 173), as with the Littoridininae, proposed the Cochliopininae as a new subfamily: both had been established by earlier authors. His work, therefore, should be regarded only as an emendation and Tryon remains the author of the subfamily. Taylor (1966) also established three new tribes in the subfamily. One of these, the Cochliopini, belongs exclusively to the western hemisphere, mainly Central America and the Caribbean. Tribes are not formally recognized herein, but changes in the perceived relationships between various genera would now alter Taylor's classification. In his arrangement only two living species of Cochliopini were known from South America. One is *Cochliopina kugleri* (Forcart, 1948), originally described from Venezuela as *Valvata* and now transferred to *Nanivitrea*. The other is the monospecific genus *Limnothauma* Haas, 1955, which lives in Lake Titicaca, Peru, and is best placed in the Littoridininae.

The new species described here as *?Nanivitrea colombiana* belongs to a small group of genera including *Cochliopa* Stimpson (1865*a*), *Subcochliopa* Morrison (1946) and *Cochliopina* Morrison (1946). Morrison distinguished between his two genera on anatomical grounds, but they do not seem easy to separate on the shell characters that he also suggested were diagnostic. As Morrison ignored the little-known *Nanivitrea* entirely, his work may need revision and the taxonomy of the group is probably unstable. The distribution of *Amnicola rowelli* Tryon (1863), the type species of *Cochliopa*, had been disputed for a long time. Morrison, after comparing the type series with material that he had collected himself, concluded that it was Panamanian and not Californian as had been originally thought, and that the three species assigned to the genus were all from the Pacific drainage of Panama and the Pearl Islands.

The best illustrations of *Cochliopa* are those of Morrison's species: unfortunately he did not refigure *C. rowelli*. Tryon's original figures were inaccurate, but Binney (1865: 73, fig. 144) provided a better drawing. Wenz (1939: 575, fig. 1561) chose *Cochliopa riograndensis* Pilsbry & Ferris (1906) as his example of the genus: this is now the type species of *Cochliopina* Morrison.

Thiele (1929: 170, fig. 150) provided probably the first illustration of *Paludinella helicoides* Gundlach (*in* Poey, 1865: 70), the type species of *Nanivitrea*, and described it as translucent. Unfortunately, he gave no details authenticating his determination.

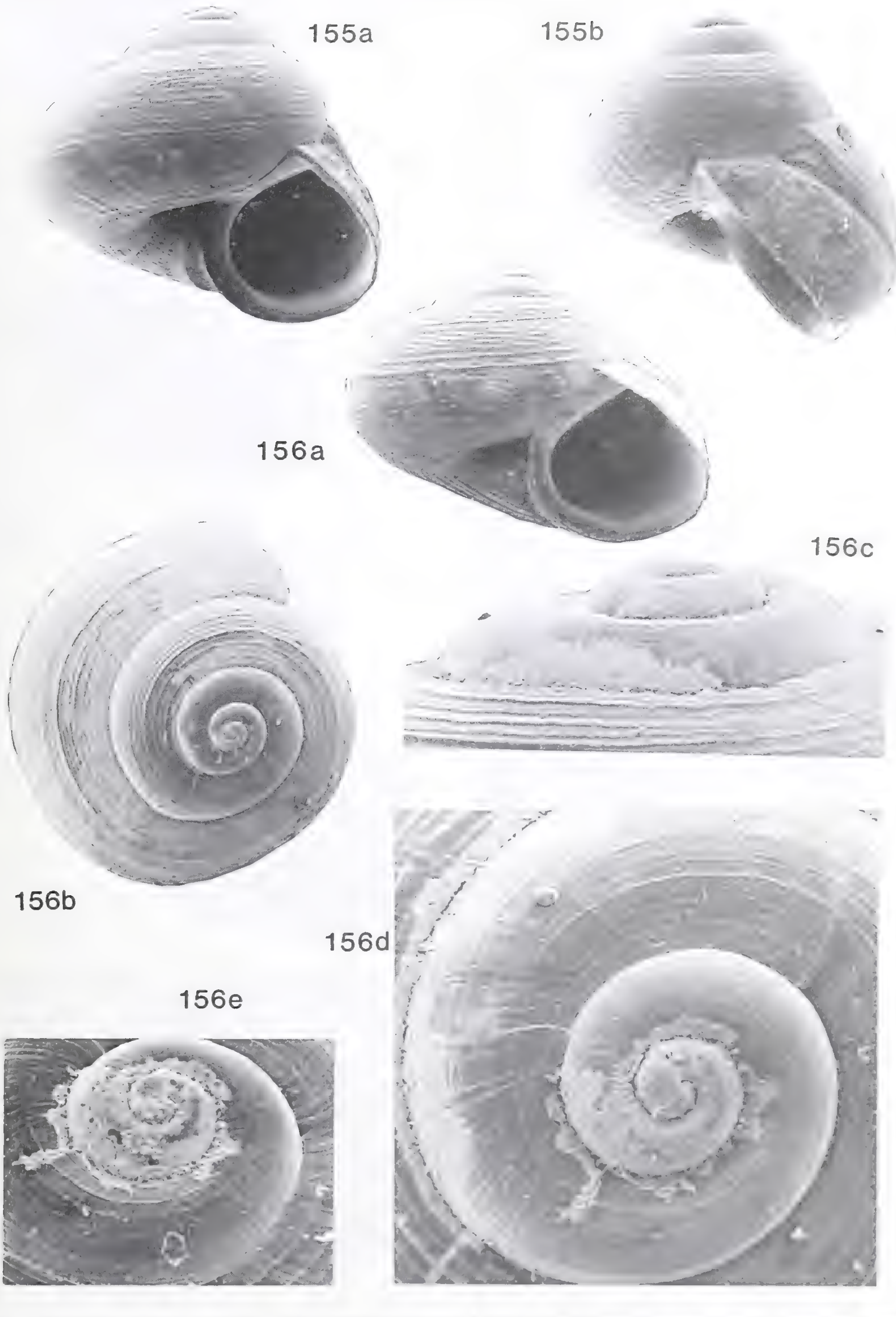
Insofar as it affects the generic assignment of the new Colombian fossil, an attempt is made below to distinguish on shell characters alone between the four genera under discussion. This is based partly on the views of both Morrison (1946) and Taylor (1966), and takes account of the features of the numerous species that they list.

Subcochliopa is restricted to shells with rather weak peripheral keeling and having slightly flattened bases. Shells are spirally lirate, sometimes with lirations obsolete on the base. The two Panamanian species described by Morrison are moderate-sized to very large, with shell heights of 3.5 mm and 7.5 mm respectively.

Cochliopa is best distinguished by its adpressed sutures, particularly between the body and penultimate whorls in adults. The shell can be smooth or finely striate and tends to be fairly large, with the height between 3.5 mm and 5.0 mm.

Nanivitrea has impressed sutures. Shells are smooth, normally translucent and small, with shell height less than 2.5 mm.

Cochliopina (Figs 155–157) is much the most widespread of these genera and is represented by about 20 species. It has impressed sutures and varies in shape between the almost planorbiform *C. hinkleyi* (Pilsbry, 1920) and the trochiform *C. izabel* (Pilsbry, 1920). The shell is normally striate, the striations being fine and of small amplitude in most species, but quite coarse in some such as *C. hinkleyi* and *C. milleri* Taylor (1966). *C. izabel* is nearly smooth, but Pilsbry (1920) described a striate 'mutation' *perstriata*. The type species, *C. riograndensis* (Pilsbry & Ferris, 1906) is broadly heliciform and weakly striate and thus intermediate for these characters. In common with most other species assigned to the genus it is small, with a height of about 2.0 mm and a breadth of about 2.7 mm. A few species, particularly some described by Morrison (1946) from Panama, are much larger, *C. wetmorei*



Figs 155–156 *Cochliopina extremis* Morrison (1946). Recent; off San José Island, Pearl Islands, Panama (Pacific); paratypes, presented by Smithsonian Institution. **155**, BMZD 1951.11.1.64; a, front, × 20; b, side, × 20. **156**, BMZD 1951.11.1.65; a, front, × 20; b, apical view, × 20, c, d, e, side, vertical and oblique views of apex, all × 100.

being the largest with height and breadth both about 6.0 mm. It seems possible that the species which have been assigned to *Cochliopina* may belong to more than one genus.

Ecological conclusions drawn from the presence of members of the Cochliopini can only be tentative. All except *Subcochliopa* are known to have reached islands. Morrison (1946: 19) noted that *Cochliopa* on San José Island ranged from tidal level almost to the source of streams, whilst *Cochliopina* was limited to a narrow zone of the stream a little above tidewater. Other *Cochliopina* are clearly fresh-water only, living far from the sea, with *C. riograndensis* favouring protected situations, such as under stones and among watercress, along edges of streams (Taylor, 1966).

Both Morrison (1946) and Taylor (1966) suggested that the more northerly species of *Cochliopina* lived in streams draining eastwards into the Gulf of Mexico and the Caribbean, whilst the more southerly species from Nicaragua to Panama occur only in the Pacific drainage system. Morrison (1946: 18) thought that this separation might have originated in the palaeobiological history of the region. However, the value of such observations is seriously reduced, both by doubts as to whether the genus is monophyletic and by considerable gaps in collecting of both fossil and Recent material. If Taylor's assignment of *Valvata kugleri* to *Cochliopina* were to be accepted, it would make it the only South American (Venezuelan) member of the northern group which lives in the Atlantic drainage system.

Genus ***NANIVITREA*** Thiele, 1927

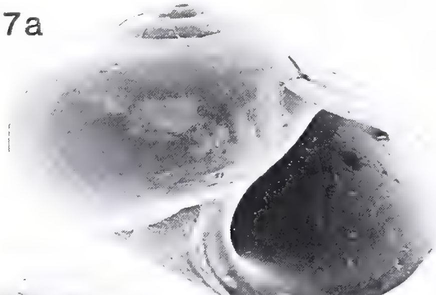
Type species. *Paludinella helicoides* Gundlach *in* Poey, 1865: 70. Recent, Cuba. By monotypy.

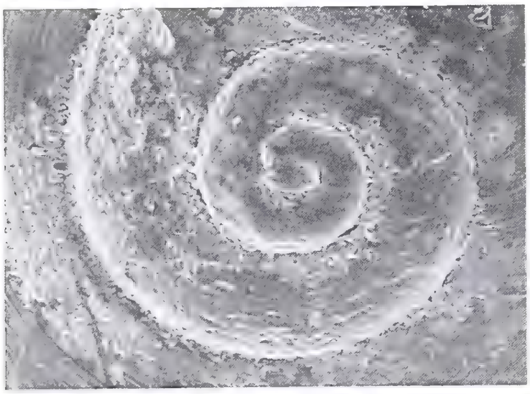
Diagnosis. Like *Cochliopa* but with small, smooth and often translucent shell seldom exceeding 2.5 mm in height; sutures impressed.

Other species assigned. Recent: *Nanivitrea alcaldei* Jaume & Abbott (1948: 5), Cuba; *Valvata inconspicua* C. B. Adams (1851: 131), Jamaica; *Valvata pygmaea* C. B. Adams (1849: 42), Jamaica; *Valvata kugleri* Forcart (1948: 50), Venezuela. Fossil, first record herein, Late Caenozoic, La Tagua, Colombia: *Nanivitrea colombiana* sp. nov.

Generic distribution. Recent, Cuba, Jamaica, Venezuela. Late Caenozoic, Colombia.

157a





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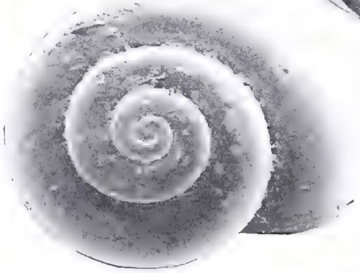

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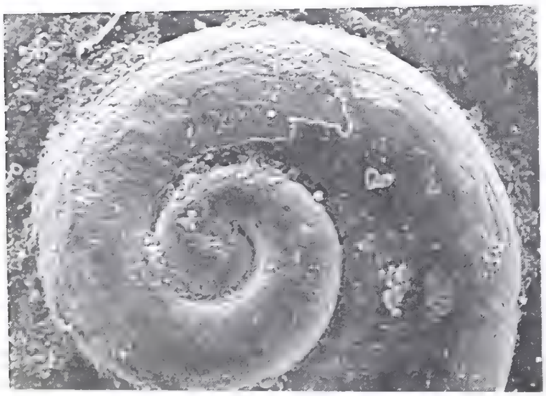
158b



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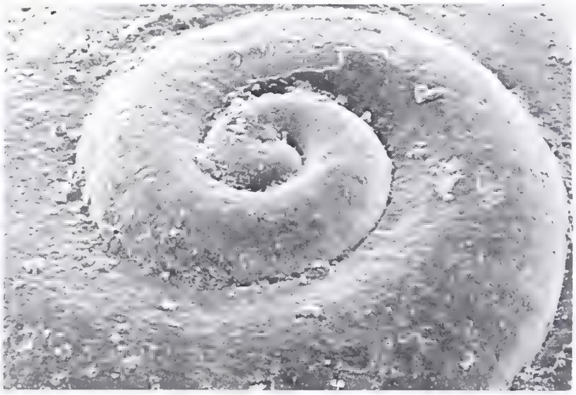
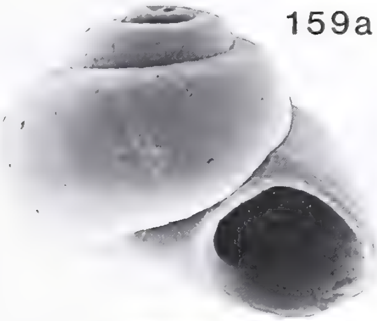


Fig. 157 *Cochliopina diazensis* Morrison (1946). Recent; Panama; paratype, presented by Smithsonian Institution, BMZD 1951.11.1.81; a, front, × 20; b, vertical view of apex, × 100.

Fig. 158 *Nanivitrea colombiana* sp. nov. Neogene; 1.5 km upstream from La Tagua, Colombia; Weeda Colln. Paratype, GG19891; a, apical view, × 20; b, same, × 100; c, oblique view of apex, × 100.



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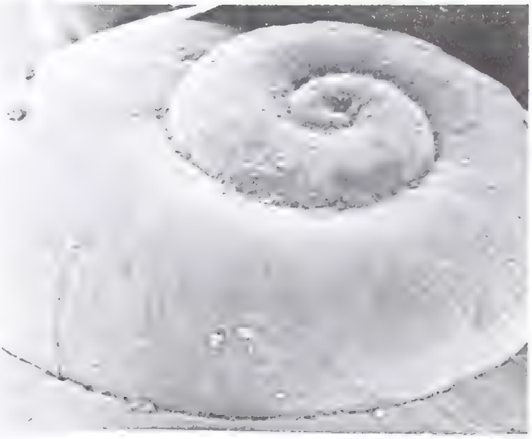

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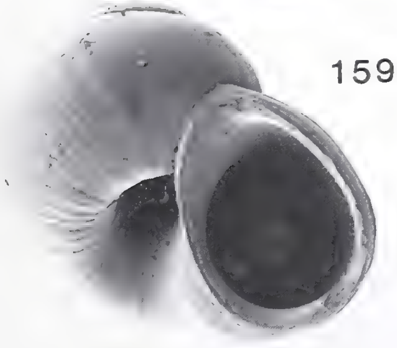

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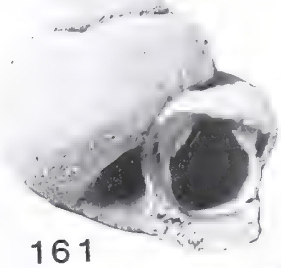

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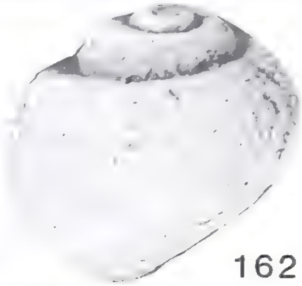

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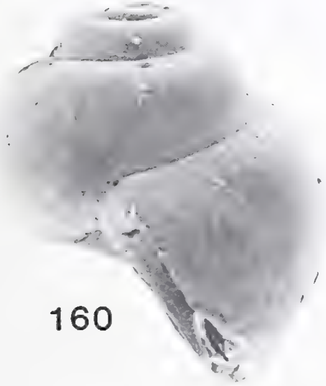

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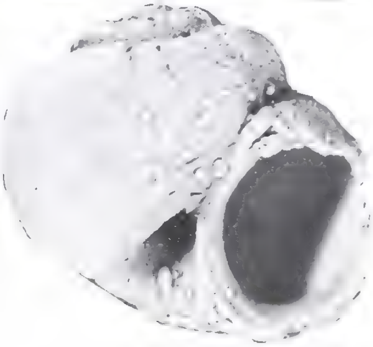


163

Figs 159–163 *Nanivitrea colombiana* sp. nov. Late Caenozoic; La Tagua, Colombia. **159–160**, 1.5 km upstream from La Tagua, Weeda Colln. **159, holotype**, GG19887; a, front, × 25; b, obliquely from below, × 25; c, apical whorls, × 90. **160**, paratype, GG19889; side, × 25. **161–163**, Eden Colln. **161–162**, paratypes, Loc.33/480–560. **161**, GG19925/1; front, × 12.5. **162**, GG19925/2; rear, × 20. **163**, paratype, Loc. 54, GG19927/1; front, × 20.

REMARKS. Possible relationships with other cochliopinids are discussed above. *Valvata kugleri* was reassigned to *Cochliopina* by Taylor (1966) but, as it is both smooth-shelled and translucent, seems better placed in *Nanivitrea*. I agree with the views of Jaume & Abbott (1948), who commented on the similarity of *Cochliopina* to *Nanivitrea*. The new species is assigned to the latter because the majority of the specimens are completely smooth. It is, however, thick-shelled and would almost certainly not have been translucent. The known distribution of the genus is discontinuous, probably because such small shells have been overlooked. However, no specimens have been found among the other micromolluscs extracted from the Pichana and Puerto Nariño samples.

Nanivitrea colombiana sp. nov. Figs 158–163

HOLOTYPE. GG19887, Late Caenozoic, 1.5 km upstream from La Tagua on Rio Caqueta, Colombia (Weeda Colln). The following are paratypes: GG19888–91 (more than 30 shells), same details as holotype; GG19925–6, Loc. 33/480–560, La Tagua (Eden Colln); GG19927–8, Loc. 54, La Tagua (Eden Colln); GG21515, Loc. 44, La Tagua (Eden Colln).

NAME. 'Colombian'.

DIAGNOSIS. Heliciform, with breadth slightly greater than height; aperture rounded below and bluntly angled above; periphery at strongly impressed suture; umbilicus deep, but not wide enough in adult to show early whorls; shell smooth except for prosocline growth lines and rare spiral threads.

DESCRIPTION. The initial whorl is either flattened or even slightly sunken. For the next two whorls the suture lies below the highest point of the rather circular-sectioned whorls. That part of the shell nearest the suture slopes abapically with the result that young shells appear planorbiform. In later growth stages, the translation rate increases and the part of the whorl adjacent to the adapical suture slopes downwards, the shell assuming a more turbiniform shape. The later whorls remain strongly convex, with the periphery lying at the impressed suture. The shell in the apertural region is thick. The aperture is slightly higher than broad. It is rounded below and bluntly angled above, with the angulation lying at about its mid-width. The rim of the deep umbilicus is well rounded, with no trace of carination. The penultimate whorl is rarely visible from below except in juvenile specimens. The growth lines are strongly prosocline. Weak and randomly positioned spiral threads are visible only in a small proportion of specimens.

DIMENSIONS. In mm.	h	br	h/br
GG19887, holotype, 1.5 km upstream of La Tagua (Weeda Colln).	2.15	2.25	0.95
GG19888, paratype, same loc.	2.1	2.2	0.95
GG19925/1, paratype, Loc. 33/480–560, La Tagua (Eden Colln).	2.8	2.9	0.96
GG19927/1, paratype, Loc. 54, La Tagua (Eden Colln)	2.4	2.4	1.0

REMARKS. *N. kugleri* (Forcart) is similar, but relatively broader (h, 1.7 mm; br, 2.4 mm; h/br, 0.7; measurements from Forcart, 1948). In addition, its whorls are more evenly convex and have their periphery slightly higher, above, and not at, the suture. Its aperture is relatively broader with the adapical angulation well to the left of mid-breadth. Forcart described it as being translucent, and his type illustrations suggest that the shell is much thinner than that of *N. colombiana*.

Because of the planorbiform shape of the early whorls, broken juvenile stages of the present species strongly resemble *Coahuilix* D. W. Taylor, 1966. Without comparative material, it is not possible to say whether this similarity is a feature of all *Nanivitrea*.

Subfamily ?**LITHOGLYPHINAE** Thiele, 1929

[Tribus Lithoglypheae Thiele, 1929: 145, *nom. transl.* Wenz, 1939: 577]

The Pebasian *Eubora*, *Toxosoma* and *Tropidobora* are here doubtfully referred to the Lithoglyphinae of the Hydrobiidae.

Thiele (1929: 141–2) placed both *Potamolithus* Pilsbry (1896: 88) and *Littoridina* Souleyet (1852: 565) in his Tribus Littoridineae. This arrangement was followed by Wenz (1939). However, Davis & Pons da Silva (1984), following an earlier study (Pons da Silva & Davis, 1983), transferred *Potamolithus* to the Lithoglyphinae, their analysis of its anatomy suggesting a close relationship to the living European *Lithoglyphus* (Hartmann, 1821). Living members of the Lithoglyphinae are known from both Europe and North America. The fossil history of the subfamily appears to be poorly known, being confined mainly to Pleistocene records. Further investigation of this and its present distribution would be necessary to explain its occurence in the La Plata region satisfactorily. However, as the fossil *Eubora*, *Tropidobora* and possibly *Toxosoma* appear to be related to *Potamolithus* on shell characters, the three former are here placed provisionally in the Lithoglyphinae.

Taylor (1966) erected the Mexithaumatinae for his new species of Hydrobiidae, *Mexithauma quadripaludium*. The strong superficial resemblance of its shell to that of *Eubora* bella (Conrad) from the Pebasian of Pichana might suggest that they are closely related, but Hershler (1985: 112, fig. 52) convincingly argued that the siphonal notch of *Eubora* was unknown in living hydrobiids.

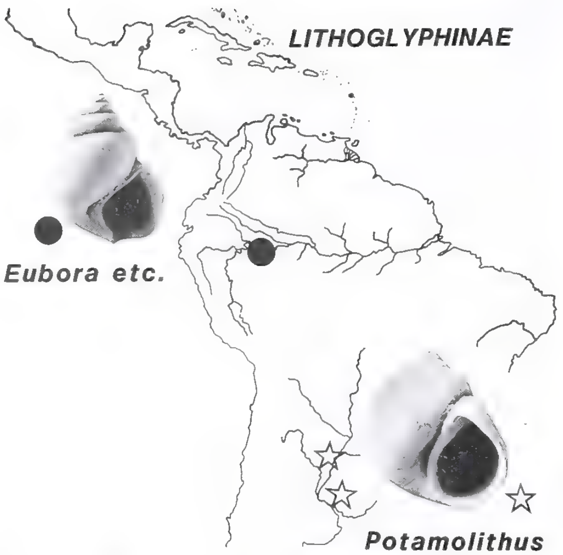


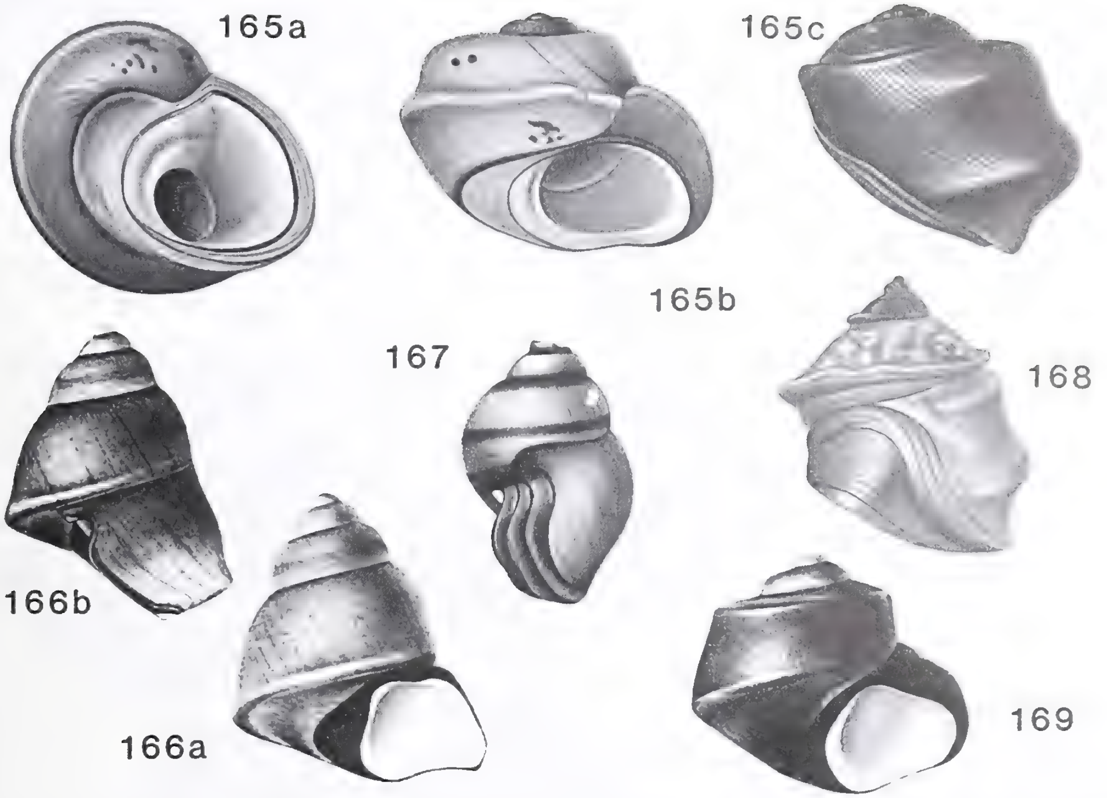
Fig. 164 Neogene and Recent distribution of Lithoglyphinae. ●, fossil *Eubora, Tropidobora* and *Toxosoma*; Pebasian Basin. ☆, Recent *Potamolithus*; Uruguay, northern Argentina and southern Brazil. Inset, *Eubora crassilabra* (Conrad), Pichana, Peru, × 2.5; *Potamolithus lapidum* (d'Orbigny), Uruguay, × 3.

Thompson (1964) assigned his living monotypic genus *Rachipteron* to the Amnicolidae (Rissoacea). His type species *R. philopelum* has some resemblance to *Eubora* in general shape, and like *E. bella*, is spirally ribbed. These ribs, however, are much more numerous and weaker than in the fossil. More importantly, *Rachipteron* also lacks the siphonal notch of *Eubora*.

Kadolsky (1980: 366) has proposed the new name *Eubora* for the preoccupied *Ebora* Conrad, 1871*b* and also decided that *Nesis* Conrad, 1871*b*, another preoccupied name, was not worthy of separation from *Eubora*. In dealing with *Toxosoma* Conrad, 1874*a*, Kadolsky concluded (1980: 372, 374) that it was closely related to *Eubora* and that both genera should, with some reservations, be placed in the Hydrobiidae, rather than regarded as related to *Lacuna* (Lacunidae of the Littorinacea) as suggested by de Greve (1938: 79).

Pilsbry (1944: 150–1, text-figs 2, 3a, b) erected *Tropidobora*, represented by a single species, *Pachytoma tertiana* Conrad, 1874*a*. He also redescribed and figured *Toxosoma* (1944: 151, text-figs 3a, b). He too had concluded that, in spite of its prominent columellar fold, *Toxosoma* was close to *Ebora*.

Both Pilsbry and Kadolsky had noted the resemblance between *Ebora*, *Tropidobora*, and the living *Potamolithus* Pilsbry (Figs 165–170), which is restricted to rivers of the Atlantic drainage system of Argentina, Uruguay and southern Brazil (Pilsbry 1911: 566–602; pls 38–41b; Parodiz 1969: 112, map 4). Pilsbry (1911) provided full and well-illustrated descriptions of numerous nominal living species from a small number of localities. His figures (1911: pl. 38, figs 1, 4) of the type species *P. rushi* Pilsbry, 1896 show the aperture to be subcircular and without any sinus or notch, except for a blunted angulation posteriorly where the inner and outer lips meet. The type material (in ANSP) came from Paysandú on



Figs 165–169 *Potamolithus*. Recent species from Uruguay also occurring in adjoining parts of Argentina. Illustrations copied from Pilsbry (1911). **165**a, b, c, *Potamolithus rushi* Pilsbry (1911: pl. 38, figs 1, 1a, 1b; type illustrations of type species of *Potamolithus* Pilsbry); Paysandú, Uruguay River; × 7.5. **166**a, b, *Potamolithus filiponei* von Ihering, figured Pilsbry (1911: pl. 41a, figs 8, 8a), Montevideo; × 8. **167**, *Potamolithus bisinuatus obsoletus* Pilsbry (1911: pl. 41, fig. 7a), gerontic paratype; Rio de la Plata, San Gabriel's Island, near Colonia, Uruguay; side view of outer lip, × 7.5. **168**, *Potamolithus microthauma* Pilsbry (1911: pl. 38, fig. 2b), a type illustration; Paysandú, Uruguay River; × 7.5. **169**, *Potamolithus quadratus* Pilsbry (1911: pl. 41a, fig. 6), a type illustration; Paysandú, Uruguay River; × 8.

the Uruguay River. Other species having apertures with broadly concave bases, but with no notch separating the columella from the base of the aperture, and with strongly sinuate outer lips, are illustrated by Pilsbry (1911). These include *P. bisinuatus obsoletus* Pilsbry (1911: 577; pl. 41, figs 3, 5) and *P. gracilis* with its subspecies *P. gracilis viridis* (1911: 577–8; pl. 41, figs 8, 9 respectively). *P. gracilis* s.str. also occurs at Paysandu, whilst both subspecies are found at San Gabriel's Island on Rio de la Plata, near Colonia, Fray Bentos, Uruguay.

Pilsbry (1911) also dealt with another group of species with broadly sinuate apertural bases, coupled with comparatively straight outer lips similar to that of the type species. These species have basal carinae which are much more strongly developed than in *P. rushi*, and are somewhat reminiscent of *Tropidobora* in general outline, though lacking the flattened base of the latter. Two of these, *P. carinifer* Pilsbry (see 1911: pl. 41A, fig. 5) and *P. quadratus* Pilsbry (1911: 592; pl. 41A, fig 6) also occur at Paysandú, the type locality of *P. rushi*. A third species, *P. filiponei* von Ihering (1910: 15) is known from Montevideo (Pilsbry 1911: 573; pl. 41A, figs 8, 8a).

It therefore seems that either the aperture of *Potamolithus* is highly variable or that the various species discussed above represent more than one genus. Their frequent co-occurrence suggests that the former explanation is the more likely, and indeed brings into question the necessity for recognizing so many species of *Potamolithus*. None of Pilsbry's excellent illustrations, nor the few largely unidentified samples of the genus in BMZD, have apertures particularly similar to those of the fossil genera under consideration. Although it seems reasonable to regard *Eubora* and *Tropidobora* as closely related, their general similarity to *Potamolithus* may be due to convergence and cannot be taken as strong evidence that all three might be grouped together.

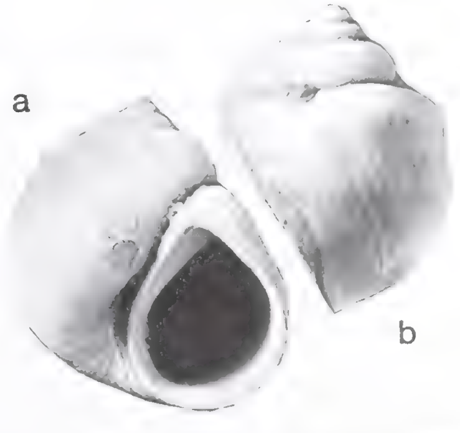


Fig. 170 *Potamolithus lapidum* (d'Orbigny), labelled as var. *supersulcatus* Pilsbry (1896: 88). Recent; San Gabriel's Island, Rio de la Plata, Uruguay (type locality); E. R. Sykes Colln, BMZD 97.2.19.1. a, front; b, side; both × 6.

As mentioned, Taylor (1966: 204) erected the monospecific subfamily Mexithaumatinae of the Hydrobiidae for his new genus and species *Mexithauma quadripaludium* Taylor (1966: 205; pl. 19, figs 58–63, text-fig. 22), which came from several fresh-water lagunas in the valley of Cuatro Cienegas, Coahuila, northern Mexico. Taylor did not compare it with either *Potamolithus* or any of the Amazon fossil genera, but its sculpture of spiral carinae is like that of *Eubora bella* (Conrad). The aperture is rounded below and pointed above. The inner lip is thickened as in *Eubora* and *Potamolithus*. Kadolsky (1980: 367), however, pointed out that it differs from *Eubora* in several important respects – having strictly prosocline growth lines, no basal apertural notch, a much less developed pseudumbilicus and no umbilical ridge. Nevertheless, as we have seen considerable variation occurs in the apertural characters of species assigned to *Potamolithus*. The presence of a columellar plait in *Toxosoma* clearly did not debar it from being considered to be closely related to *Eubora* by either Pilsbry (1944) or Kadolsky (1980). It seems, therefore, reasonable that such differences should not preclude a similarly close relationship between *Mexithauma* and the other genera under consideration. But a comparison of the anatomy of *Mexithauma*, *Lithoglyphus* and *Potamolithus* would be necessary before any firm conclusions could be drawn.

Ponder (1982) has reviewed the several Australasian and New Caledonian species of living *Hemistomia* Crosse (1872) occurring on Lord Howe Island. In the majority, the columella is simple, but in two species, columellar bulges of varying strength occur (Ponder 1982: figs 79, 80, 87). From the example of *Hemistomia* it may be argued that the columellar fold of *Toxosoma* does not preclude it from being fairly closely related to *Eubora*.

In summary, therefore, both the familial and subfamilial assignment of these Pebasian genera must remain undecided.

Genus ***EUBORA*** Kadolsky, 1980

[*nom. nov.* (Kadolsky, 1980: 366) pro *Ebora* Conrad, 1871*b*: 194, non Walker, 1867: 415.
= *Ebora (Nesis)* Conrad, 1871 (type species *Ebora (Nesis) bella* Conrad, 1871*b*: 194; Late Caenozoic, Pebasian; Pichana, Peru; by monotypy), non *Nesis* Mulsant, 1850: 67; nec Stäl, 1860: 67.]

TYPE SPECIES . *Ebora (Ebora) crassilabra* Conrad, 1871, Late Caenozoic, Pebasian; Pichana, Peru. By monotypy as type of *Ebora*.

REMARKS. This genus is dealt with in detail by Kadolsky, 1980. Only five species so far have been assigned to it: *E. crassilabra* Conrad, *E. bella* (Conrad), *E. grevei* Kadolsky, 1980, *E. pygmaea* Kadolsky, 1980, *E. woodwardi* Kadolsky, 1980. All are confined to a few Pebasian localities of the upper Amazon Basin. No full treatment of them is warranted herein. Some new informtion and a few points not fully covered by Kadolsky are given below, and the opportunity is taken to publish photographic illustrations of some important specimens, in most cases for the first time. The taxonomic position of *Eubora* is discussed above (p. 214).

Eubora crassilabra (Conrad, 1871) Figs 171–172

*. 1871*b* *Ebora (Ebora) crassilabra* Conrad: 194; pl. 10, fig. 14.
v. 1871 *Ebora crassilabra* Conrad; Woodward: 102 (*pars*; *non* pl. 5, figs 1a, b, = *E. woodwardi* Kadolsky).
? 1874*a* *Ebora crassilabra* Conrad; Conrad: 32; pl. 1, fig. 9.
. 1878 *Lacuna (Ebora) crassilabris* (Conrad) Boettger: 494; pl.13, figs 12a–d.
. 1915 *Lacuna (Pseudocirsope) crassilabris* (Conrad); Cossmann: 102.
. 1980 *Eubora crassilabra* (Conrad) Kadolsky: 367; figs 3, 4 (*cum syn*).
1980 *Eubora* cf. *E. crassilabra* (Conrad) Kadolsky: fig. 5.
. 1980 *Lacuna (Ebora) crassilabris* (Conrad); Costa: 885; pl. 2, figs 7–10.

HOLOTYPE. NYSM 9194, Late Caenozoic, Pebasian; probably Pichana (Hauxwell Colln). Not studied herein.

MATERIAL STUDIED. All from type locality and horizon (Hauxwell Colln), studied by Woodward (1871): G25297 (8 shells); GG19830/1–25 (GG19830/1 original of Kadolsky, 1980: fig. 4); GG19836, original of Kadolsky, 1980: fig. 5.

FURTHER OCCURRENCES. Late Caenozoic, Pebasian, afloramento em Atalaia do Norte; CPCAN I, Tamanduá; CPCAN III, São Paulo de Olivença, Alto Amazonas, Brazil (Costa 1980: 885).

DIMENSIONS. In mm.	h	br	hap	h/br	sa
GG19830/1 (Kadolsky 1980: fig. 4)	8.2	6.0	–	1.37	63°
GG19830/2	6.7	5.2	3.7	1.29	63°

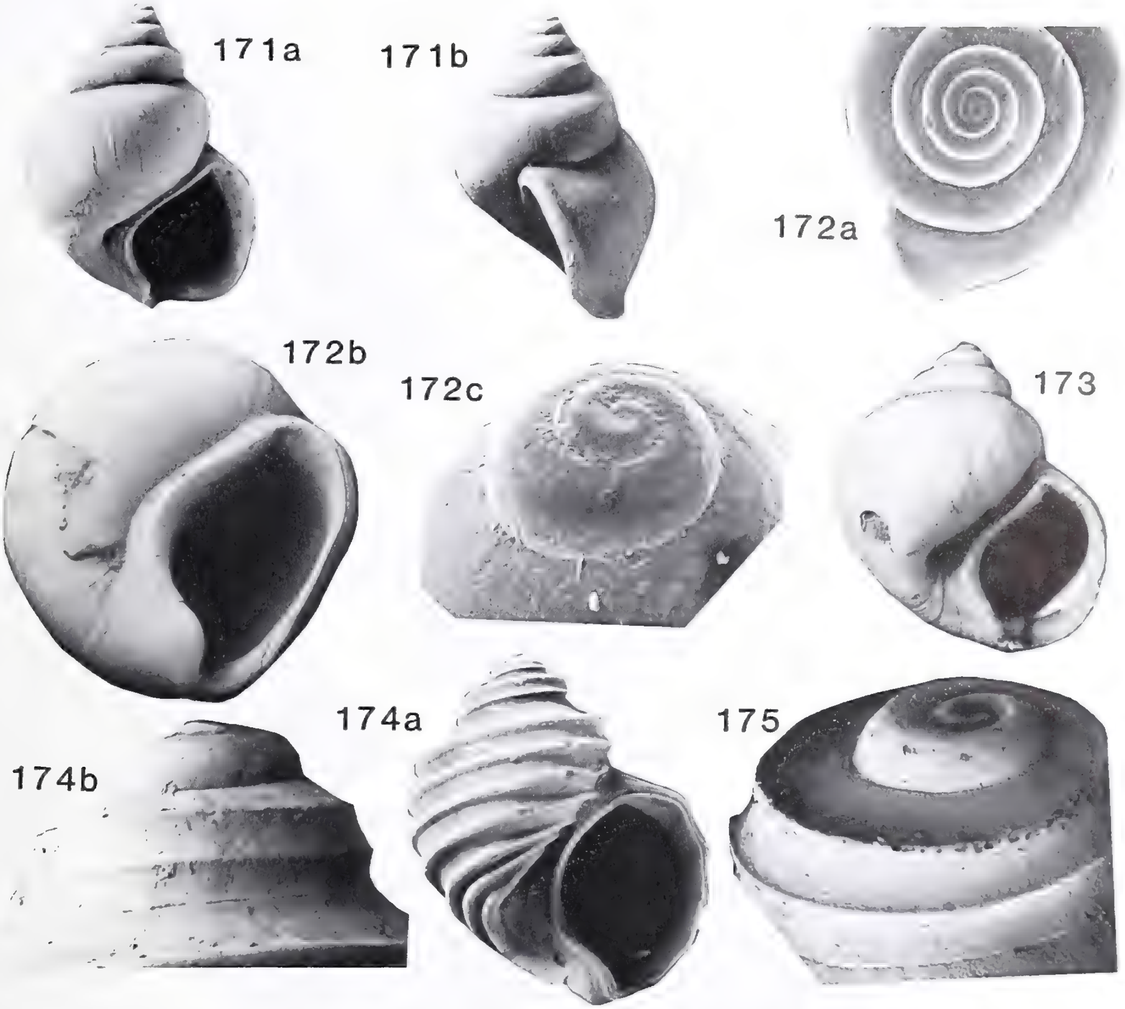
REMARKS. The records of Costa (1980) are from new Pebasian localities lying to the east of the area from which the species was previously known, but they do not alter its known stratigraphical distribution. Costa later (1981) recorded and provided correctly identified figures of *E. woodwardi* from elsewhere (see below); her 1980 record of *E. crassilabris* can therefore be accepted with confidence. *E. crassilabris* is best distinguished from *E. woodwardi* by its less squat form and more vertical columella: that of the latter species is strongly curved to the right.

Eubora woodwardi Kadolsky, 1980 Fig. 173

v. 1871 *Ebora crassilabra* Conrad; Woodward: 102 (*pars*); pl. 5, fig. 1a, b.
. 1924 *Ebora crassilabra* Conrad; Roxo: 47.
*v 1980 *Eubora woodwardi* Kadolsky: 368, figs 6–8 (*cum syn.*).
. 1981 *Eubora woodwardi* Kadolsky; Costa: 641; pl. 1, figs 5, 6.

HOLOTYPE. GG19831/1, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln), the specimen figured both by Woodward (1871) and Kadolsky (1980): see also p. 355. Dimensions (mm): h, 7.6; br, 6.5; hap, 3.9; h/br, 1.17; sa, 84°. Four paratypes, GG19831/2–5, and six other shells, GG19831/6–11 not quoted by Kadolsky, were also studied. All from same horizon, locality and collection.

FURTHER RECORD. Late Caenozoic; Três Unidos, Peru (Roxo 1924, Costa 1981). Prior to the recognition of this species here by Costa (1981), it was believed (Kadolsky 1980) to be confined to Pichana and Iquitos.



Figs 171–175 Species of *Eubora*. All Pebasian; Pichana, Peru; Hauxwell Colln. **171–172**, *Eubora crassilabra* (Conrad). **171**, GG19830/1; a, front, × 5; b, side, × 5. **172**, GG19830/2; a, apical view, × 10; b, obliquely ventral view into aperture, × 12; c, oblique view of apex, × 50. **173**, *Eubora woodwardi* Kadolsky. GG19833/1, holotype, figured by Woodward (1871: pl. 5, figs 1a, b) as *Ebora crassilabra* Conrad and by Kadolsky (1980: fig. 6); front, × 6. **174–175**, *Eubora bella* (Conrad). **174**, GG19832/1; a, front, × 5; b, side view of apex, × 30. **175**, GG19832/2; oblique view of apex, × 50.

Eubora bella (Conrad, 1871) Figs 174–175

*. 1871*b* *Ebora (Nesis) bella* Conrad: 194; pl. 10, fig. 17.
v. 1871 *Ebora (Nesis) bella* Conrad; Woodward: 102; pl. 5, fig. 3.
. 1878 *Lacuna (Ebora) bella* (Conrad) Boettger: 494; pl. 13, fig. 3.
*. 1878 *Lacuna (Ebora) bella* (Conrad) var. *semisculpta* Boettger: 495; pl. 13, fig. 2.
. 1915 *Fossarus bellus* (Conrad) Cossman: 88.
. 1938 *Lacuna (Ebora) bella* (Conrad); de Greve: 72.
. 1980 *Eubora bella* (Conrad) Kadolsky: 369 (*cum syn.*), figs 9, 10.
. 1985 *Eubora bella* (Conrad); Hershler: fig. 52.

HOLOTYPE. NYSM 9193, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln). Not seen, studied by Kadolsky, 1980; refigured by Hershler, 1985.

MATERIAL STUDIED. GG19832/1–5 (*ex* G25475–80), also studied by Kadolsky (1980); Pichana, Peru (Hauxwell Colln). Dimensions (mm), GG19832/1: h, 8.7; br, 6.2; hap, 4.0; h/br, 1.40; sa, 85°.

DISTRIBUTION. Pichana (Conrad 1871*b*, Woodward 1871); ? Pebas (Boettger 1878).

REMARKS. Kadolsky (1980) studied all the previously figured specimens of this species (Conrad 1871*b*, Woodward 1871, Boettger 1878). He pointed out that Boettger's material had also been collected by Hauxwell and assumed that it therefore came from Pichana. Boettger, however, had stated that his specimens came from Pebas: for further discussion on the probable locality for Boettger's material see p. 323.

Woodward's figure was a copy of Conrad's. He stated that he possessed no specimens of this species, but five shells (GG19832/1–5) are present in BMPD.

E. bella bears a strong, probably superficial, resemblance to the living Mexican *Mexithauma quadripaludium* Taylor, 1966. The significance of this is dealt with in the discussion on possible generic relationships above, p. 216. The distinctions between the two are mainly in the apertural region. *E. bella* possesses a siphonal notch, which results in the formation of what Kadolsky refered to as the 'umbilical ridge', and it is falsely umbilicate. *E. grevei* Kadolsky is smaller and sculptured with weak axial ribs rather than carinae.

Eubora bella is very rare. In addition to those specimens quoted herein, Kadolsky mentioned only the two shells studied by Boettger (in Senckenburg Museum, Frankfurt). No further specimens were obtained from washings of Pichana matrix in BMPD.

Eubora grevei Kadolsky, 1980

. 1938 *Lacuna (Ebora) crassilabris* (Conrad); de Greve: 70 (*pars*); pl. 5, figs 19–21, 23 (not fig. 22).
*. 1980 *Eubora grevei* Kadolsky: 369, fig. 11.

This rare species is known only from the Late Caenozoic, Pebasian of Iquitos, Peru. A comparison with *E. bella* is given above. The holotype, PIMUZ J/4 (de Greve, no. 266), was not one of de Greve's figured specimens. Its height is 6.4 mm, and breadth 5.0 mm. Kadolsky assigned de Greve's fig. 22 to *E. woodwardi*.

Eubora pygmaea Kadolsky, 1980

. 1938 *Lacuna (Ebora) crassilabris* (Conrad); de Greve: 70 (*pars*).
*. 1980 *Eubora pygmaea* Kadolsky: 371, fig. 12.

The holotype, PIMUZ J/2 (de Greve, no. 249) is the only specimen known, and was not figured by de Greve. It is from the Late Caenozoic, Pebasian of Iquitos, Peru. Kadolsky pointed out that, although only half the size of *E. crassilabra* (h, 4.8 mm; br, 3.7 mm), the apertural characters of the genus are fully developed.

Genus ***TROPIDOBORA*** Pilsbry, 1944

TYPE SPECIES. *Pachytoma tertiana* Conrad, 1874*a*, Late Caenozoic, Pebasian; type locality uncertain, either Pebas, Old Pebas or Pichana. By original designation. No other assigned species.

DIAGNOSIS. Moderately thick-shelled, with four to six whorls; trochiform, conical, with basal carina and almost flat base of shell; aperture subrectangular with broad basal sinus; columella bent to the right; thick layer of shell present along inner lip, separating columella from aperture; inner and outer lips meeting adapically at rounded, rather obtuse, angulation, outer lip smooth within; not umbilicate, but slightly indented.

REMARKS. The apertural features of *Tropidobora* and *Eubora* are identical except for the profiles of their outer lips and bases. The two genera are here regarded as separate as no species with shell outlines between the conical *Tropidobora* and convex-whorled *Eubora* are yet known. The few species of Recent *Potamolithus* in BMZD lack the broad basal sinus of the two fossil genera. However, this character is present in other species originally assigned to *Potamolithus* by Pilsbry. It seems possible, as Kadolsky (1980: 367) suggested, that not all of these species are congeneric.

Parodiz (1969: 122) assigned *Tropidobora* to the Nymphophilinae (Taylor, 1966) after examining several hundred specimens of the living Mexican *Nymphophilus minckleyi* Taylor (1966: 199, figs 17–19), the only species then assigned to that subfamily which has, however, since been expanded to include North American genera (Thompson 1977, Hershler 1985). Taylor's figures show that there are important differences between the two, particularly in the aperture. *Nymphophilus* lacks the strong notch in the outer half of the basal lip which is so characteristic of *Tropidobora*. It is considered here that the two are not closely related, beyond both belonging to the Hydrobiidae.

Both *Brachypyrgulina* and *Limnothauma* Haas, 1955 (Recent, Lake Titicaca) have shells with some resemblance to *Tropidobora*. However, they lack its broad basal apertural notch and remain assigned to the Littoridininae.

Tropidobora tertiana (Conrad, 1874) Figs 176–178

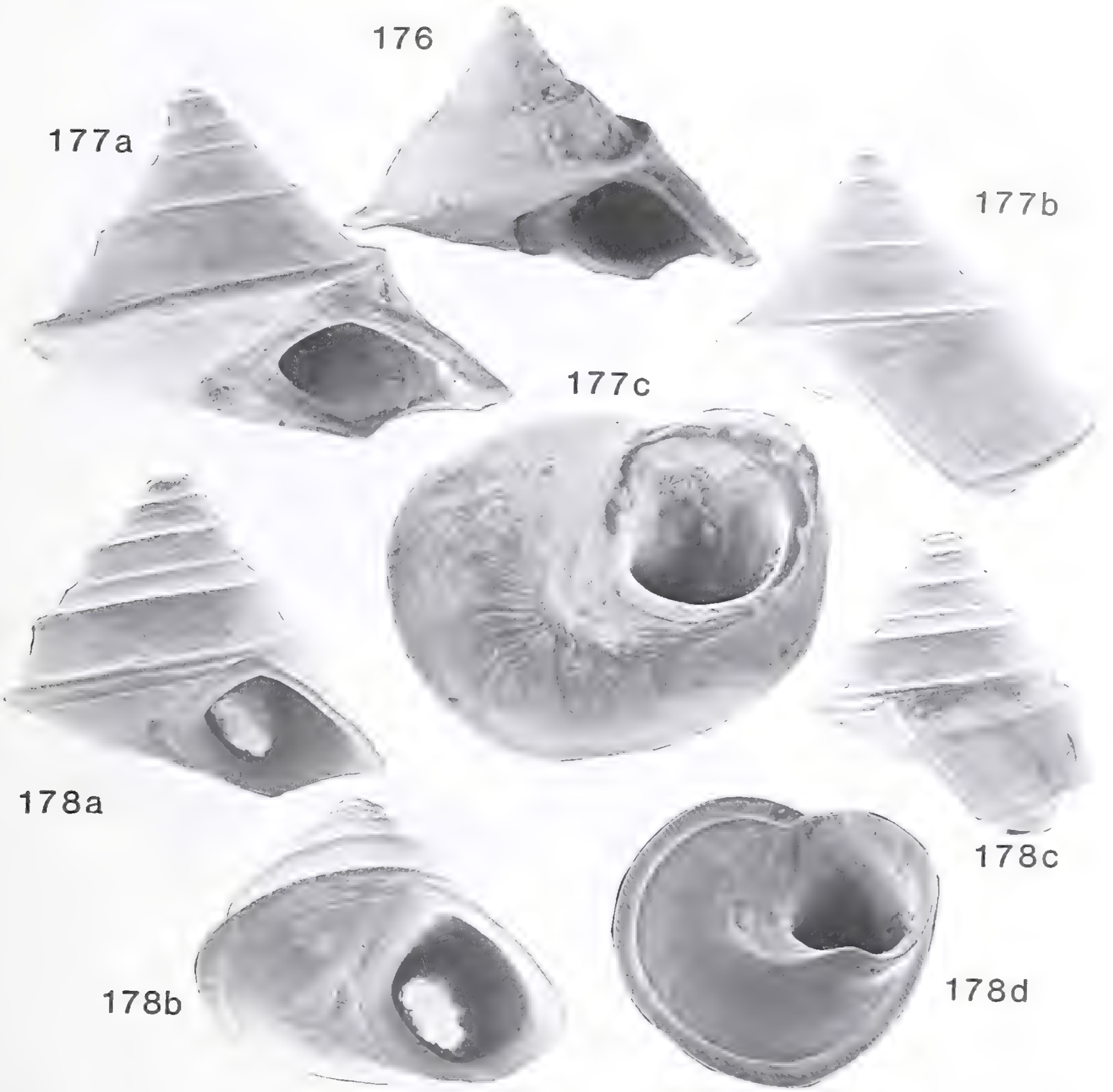
*v 1874*a* *Pachytoma tertiana* Conrad: 31; pl. 1, fig. 11.
. 1930 *Helicina? tertiana* (Conrad) Wenz: 3022.
. 1938 *Helicina? tertiana* (Conrad); de Greve: 68; pl. 4, figs 26–28, 31.
v 1944 *Tropidobora tertiana* (Conrad) Pilsbry: 150, text-fig. 2.
. 1969 *Tropidobora tertiana* (Conrad); Parodiz: 122.

HOLOTYPE. ANSP 16151, Late Caenozoic, Pebasian; either Pebas, Old Pebas or Pichana (Steere Colln).

OTHER MATERIAL STUDIED. G25294, G25295/1–3, GG21630 and also (extracted from washings, 1982) GG19995/1–4. All Late Caenozoic, Pebasian, Pichana (Hauxwell Colln). Also recorded from Iquitos (de Greve, 1938). Rare.

DIAGNOSIS. As for genus.

DESCRIPTION. There are between five and six whorls, including the apex. The first whorl is small and has a strongly convex profile. The second whorl is considerably larger and develops a high carinate shoulder, below which the whorl side is almost vertical, though the periphery lies at the lower suture. The carina rapidly drops to just above mid-whorl height during the next whorl and weakens considerably. By the penultimate (fourth or fifth) whorl this carina becomes obsolescent and by the final whorl it has disappeared altogether. On the early post-apical whorls the carina causes the whorl profile to be biconcave. The whorls are also carinate at both their upper and lower sutures, so that the later whorls have concave profiles. In contrast to the median carina, both the upper and lower sutural carinae increase in strength with growth of the shell and a flange is formed at the periphery of the final whorl. In G25294, an extra, weak, spiral thread is present on the side of the third whorl at about a third whorl height. It leaves no trace on later whorls though the mid-whorl carina persists as far as the aperture. A spiral thread is present on the base of the final whorl of this shell only. In all specimens the base of the shell is weakly convex. The apertural features are described in the generic diagnosis. The growth lines are weak. On the sides of the whorl, they are prosocline and virtually straight: as far as can be seen they are not deflected where they cross either the mid-whorl or sutural carinae. On the base of the shell, they are sigmoid, running parallel to the apertural margin, including the broad sinus. The inner margin of the basal sinus has a slightly angular junction with the base of the curved columella. This is the lowest portion of the shell and it forms a slightly angular ridge around the concavity at the axis of the shell.



Figs 176–178 *Tropidobora tertiana* (Conrad). Pebasian; Peru. **176**, ANSP 16151, holotype (of *Pachytoma tertiana* Conrad) figured by Conrad (1874*a*: pl. 1, fig. 11) and by Pilsbry (1944: text-fig. 2); either Pebas, Old Pebas or Pichana; Steere Colln; front, × 10. **177**, GG21630; Pichana; Hauxwell Colln; a, front; b, side; c, base; all × 10. **178**, G25294; Pichana; Hauxwell Colln; a, front, × 10; b, oblique view of base, × 10; c, side view, × 8; d, base, × 8. (This specimen was unfortunately destroyed before figures c and d could be repeated).

DIMENSIONS. In mm.	h	br	h/br	sa
Holotype, ANSP 16151	4.5	5.7	0.79	80°
G25294	5.0	5.2	0.96	65°
GG21630	5.3	5.7	0.93	75°

Note. Because the peripheral flange increases in relative strength with growth, the spire angle becomes more obtuse with growth. The figures given are the maximum.

REMARKS. This rare species cannot be confused with any other South American Caenozoic or Recent gastropod. Differences between it and some species of the living *Potamolithus* are discussed above (p. 215).

Genus *TOXOSOMA* Conrad, 1874*a*

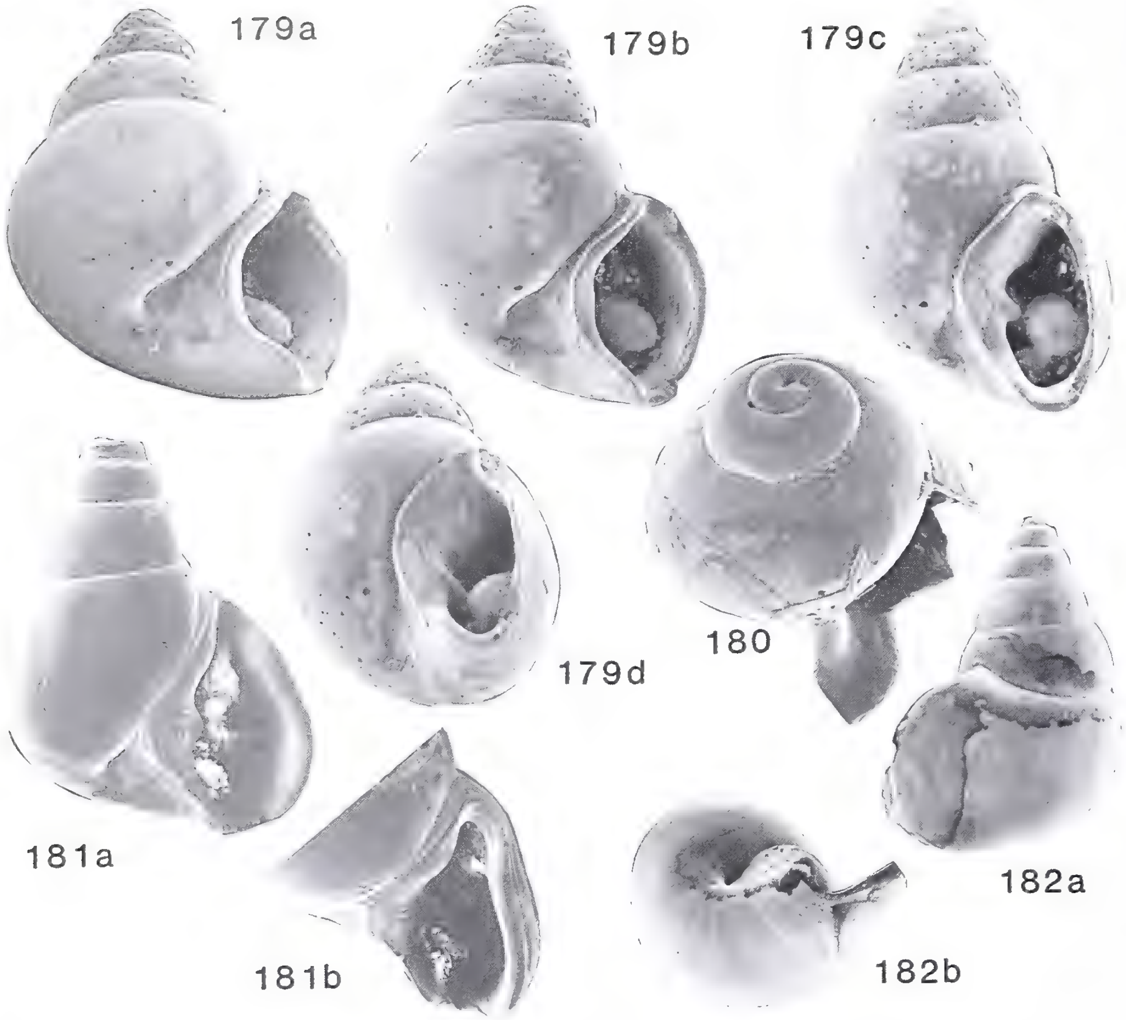
[= *Liosoma* Conrad, 1874*a*: 31 (type species *Liosoma curta* Conrad, 1874*a*: 31; Pebasian; Pebas, Old Pebas or Pichana. By monotypy); = *Pseudolacuna* Boettger, 1878: 495 (type species *Pseudolacuna macroptera* Boettger, 1878: 496; Pebas. By monotypy); = *Alycaeodonta* Etheridge, 1879: 85 (footnote), a *nomen nudum*, and acknowledged as a synonym of *Pseudolacuna* by Etheridge himself.]

TYPE SPECIES. *Toxosoma eboreum* Conrad, 1874*a*: 31; Late Caenozoic, Pebasian; Pebas, Old Pebas or Pichana. By monotypy, no other species assigned.

Confined to Late Caenozoic, Pebasian, of the Upper Amazon Basin. The suprageneric position of *Toxosoma* is discussed on p. 216 under Lithoglyphinae.

Toxosoma eborea Conrad, 1874*a* Figs 179–184

*. 1874*a* *Toxosoma eborea* Conrad: 31; pl. 1, fig. 7.
*. 1874*a* *Liosoma curta* Conrad: 31; pl. 1, fig. 8.
*. 1878 *Pseudolacuna macroptera* Boettger: 416; pl. 13, figs 14, 15.



Figs 179–182 *Toxosoma eborea* Conrad. Pebasian; Peru. **179–180**, Pichana; Hauxwell Colln. **179**, GG19835; a–d, four views to show details of apertural region, all × 15. **180**, GG21636; oblique view of apex of juvenile shell, × 50. **181–182**, Canamá; Barrington Brown Colln (these shells were not figured by Etheridge, 1879). **181**, GG19834/3; a, front view; b, oblique view into aperture; both × 12. **182**, GG19834/2; a, rear; b, base; both × 10.

v. 1879 *Pseudolacuna macroptera* Boettger; Etheridge: 85; pl. 7, fig. 12.
. 1915 *Pseudolacuna macroptera* Boettger; Cossmann: 107; pl. 12, figs 27–30.
. 1924 *Pseudolacuna macroptera* Boettger; Roxo: 47.
. 1938 *Pseudolacuna macroptera* Boettger; de Greve: 74; pl. 5, figs 17, 18, 24–29, 31–36.
. 1944 *Toxosoma eborea* Conrad; Pilsbry: 151, figs 3a, b.
. 1969 *Toxosoma eborea* Conrad; Parodiz: 121.
. 1980 *Toxosoma eborea* Conrad; Kadolsky: 373, figs 15–17 (v fig. 16)
. 1980 *Pseudolacuna macroptera* Boettger; Costa: 886; pl. 3, figs 1–6.
. 1981 *Toxosoma eborea* Conrad; Costa: 642; pl. 1, figs 7, 8.

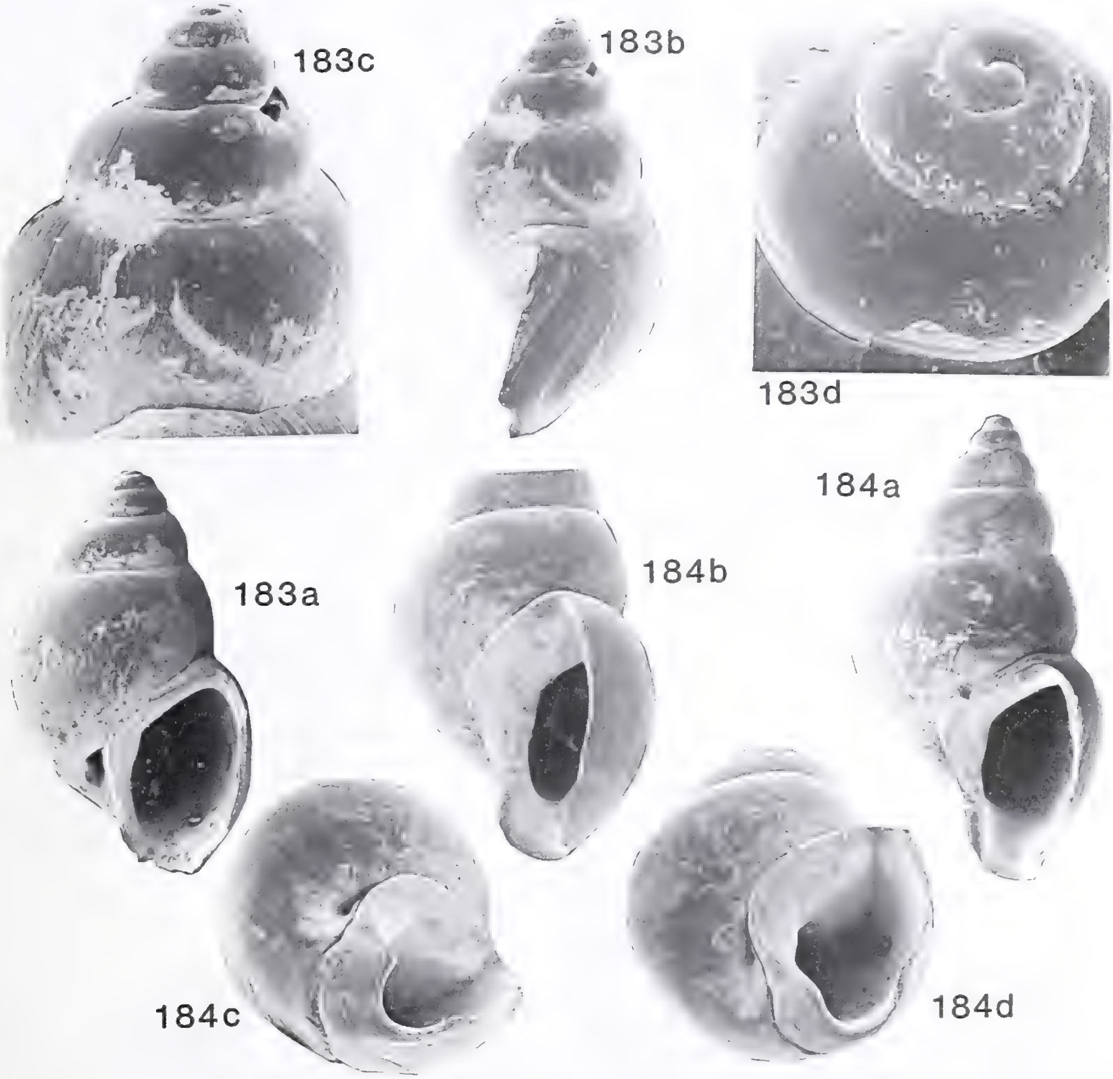
HOLOTYPE of *Toxosoma eborea* Conrad, ANSP 161152, Late Caenozoic, Pebasian; Pebas, Old Pebas or Pichana (Steere Colln), redescribed and refigured by Pilsbry (1944).

Holotype of *Liosoma curta* Conrad, same locality details as *Toxosoma eborea*, presumed lost, not listed as present in ANSP by Richards (1968).

Holotype of *Pseudolacuna macroptera* Boettger, Collection de Paléontologie, Université de Paris, 15485; Late Caenozoic, Pebasian; probably Pichana (Hauxwell Colln), refigured by Cossmann (1915) and Kadolsky (1980); not studied.

MATERIAL STUDIED. Late Caenozoic, Pebasian; GG19834/1, figured both by Etheridge (1879: pl. 7, fig. 12) and Kadolsky (1980: fig. 16) and two accompanying, unfigured shells, GG19834/2, 3, Canamá (C. B. Brown Colln, *ex* BMPD 97727); GG21513, Canamá (C. B. Brown Colln, extracted from matrix 1984); GG19853/1–6, G25481–6, Pichana (Hauxwell Colln) and GG19956/1–6, GG21635–8, Pichana (Hauxwell Colln, extracted 1982); GG19990–9, numerous specimens, Puerto Nariño, Colombia (Weeda Colln).

FURTHER OCCURENCES. All late Caenozoic, Pebasian: Três Unidos (Roxo 1924, Costa 1981); Iquitos (de Greve 1938); Rio Napo at mouth of Rio Mazan, about 30 km N of Iquitos (Willard 1966); CPCAN I, Tamandui, CPCAN III, Afloramento em Atalaia do Norte (Costa 1980). The record from the Neogene of the Cuenca Basin, Ecuador (Bristow & Parodiz 1982) is not accepted. Late Caenozoic, Pebasian; Upper Amazon Basin only.



Figs 183–184 *Toxosoma eborea* Conrad. Pebasian; Puerto Nariño, Colombia; Weeda Colln. **183**, GG19990; a, front, × 10; b, side, × 10; c, upper spire from side, × 20; d, oblique view of apex, × 50. **184**, GG19991; a, front, × 10; b, side, × 10; c, base, × 12.5; d, oblique view of base, × 12.5.

DIMENSIONS. In mm.	h	br	hap	sa
GG19835/1, Pichana.	4.1	(2.9)	2.0	53°
GG21635, Pichana.	3.8	2.2	–	–
GG21636, Pichana.	1.2	–	–	–
GG19834/1, Canamá (fig'd Etheridge, 1879: pl.1, fig. 7).	4.7	(3.7)	2.6	48°
GG19834/2, Canamá.	4.5+	(3.5)	2.5	45°
GG19834/3, Canamá.	4.3+	(3.3)	2.4	40°
GG19990, Puerto Nariño.	5.5	3.2	2.9	50°
GG19991, Puerto Nariño.	6.0	3.6	3.1	50°

Note. Breadth measurements in brackets include the apertural wing. Height to breadth ratios of this species are not given because the wing introduces a variable factor.

REMARKS. Kadolsky (1980) has redescribed this species in detail, but gave no dimensions. The illustrations in Costa (1981) confirm Roxo's earlier (1924) record from Três Unidos. The numerous specimens obtained from Puerto Nariño tend to be relatively large and also have rather convex whorl profiles and comparatively weak columellar folds. Unfortunately the wing-like outer lip of these shells is invariably broken. Nevertheless, they appear to be close enough in all essential features to be considered as belonging to the same species as the shells from Pichana in BMPD. In specimens from both Pichana and Puerto Nariño, the growth lines are extremely sinuous, particularly on the last whorl during growth of which the outer lip becomes increasingly produced. An umbilicus is present even in comparatively large immature specimens: it becomes plugged only in the late growth stages. The columellar plait dies away just before it reaches the inner lip, and is therefore often rather difficult to see in mature specimens with strongly produced outer lips. Broken specimens reveal that the columellar plait is present on earlier whorls and is not resorbed as growth proceeds.

Kadolsky (1980) appears to be correct in regarding *Liosoma curta* Conrad, 1874*a*, as a member of this species which is not fully grown.

The specimen GG19816 (Fig. 185), from the Miocene of the Cuenca Basin, Ecuador, identified as this species by

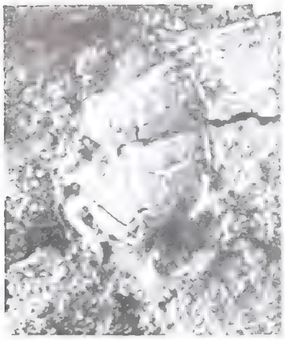


Fig. 185 Indeterminate gastropod, figured as *Toxosoma eboreum* by Bristow & Parodiz (1982: 42, fig. 16). Miocene, Mangán Formation; Loc. CRB 36, Cuenca Basin, Ecuador; GG19816, × 10.

Parodiz (*in* Bristow & Parodiz, 1982: 41, fig. 16) is not a *Toxosoma*. It has moderately coarse axial ribbing and indistinct traces of spiral threads. Both it and GG19815 come from the Mangán Formation at Loc. 36b, not 26b as quoted by Parodiz. G43325–6 (Carrion Colln), from the San Cayetano Formation of the Loja Basin, Ecuador, were labelled by Parodiz as belonging to this species, but were not mentioned in Bristow & Parodiz (1982). The material consists of blocks of well-bedded buff marl rich in moulds of small gastropods which resemble this species in shape. They are, however, considerably smaller, with a maximum height of 2 mm, and have much smaller whorls. Unfortunately neither the shape of their growth lines nor the presence or absence of a columellar plait can be made out. Although these specimens might be *Toxosoma*, they are much more likely to be very young 'post-spat' of the smooth-spired *Heleobia*, which is common at certain horizons in the Ecuadorian non-marine Neogene.

Family **VITRINELLIDAE** Bush, 1897

I am indebted to Dr W. F. Ponder (Australian Museum, Sidney) for the suggestion that the Pebasian fossil taxa dealt with below are best assigned to the otherwise fully marine family Vitrinellidae (Bush 1897: 122) rather than, as I had originally thought, to the fresh-water genus *Coahuilix* (Hydrobiidae). These fossil species, not necessarily congeneric at first sight, also bear some resemblance to the basommatophoran Superfamily Glaciodorbacea. In addition, earlier references in the literature to Pebasian species of *Planorbis* refer, at least in part, to the fossil taxa under consideration. The presence of small, virtually planorbiform, shells in several major groups means that correct familial, and even superfamilial, assignment is often indeterminate. Such shells tend to show comparatively few diagnostic features and the anatomy of many of the living taxa has not been fully investigated.

Several genera normally assigned to the Vitrinellidae are best referred to the Trochacea. N. J. Morris (BMPD) states (personal communication) that preliminary examination has shown the presence of nacre in some of these taxa: on these grounds alone, they cannot belong to the Rissoacea. This adds to the difficulties of interpreting both the living and fossil representatives of the family.

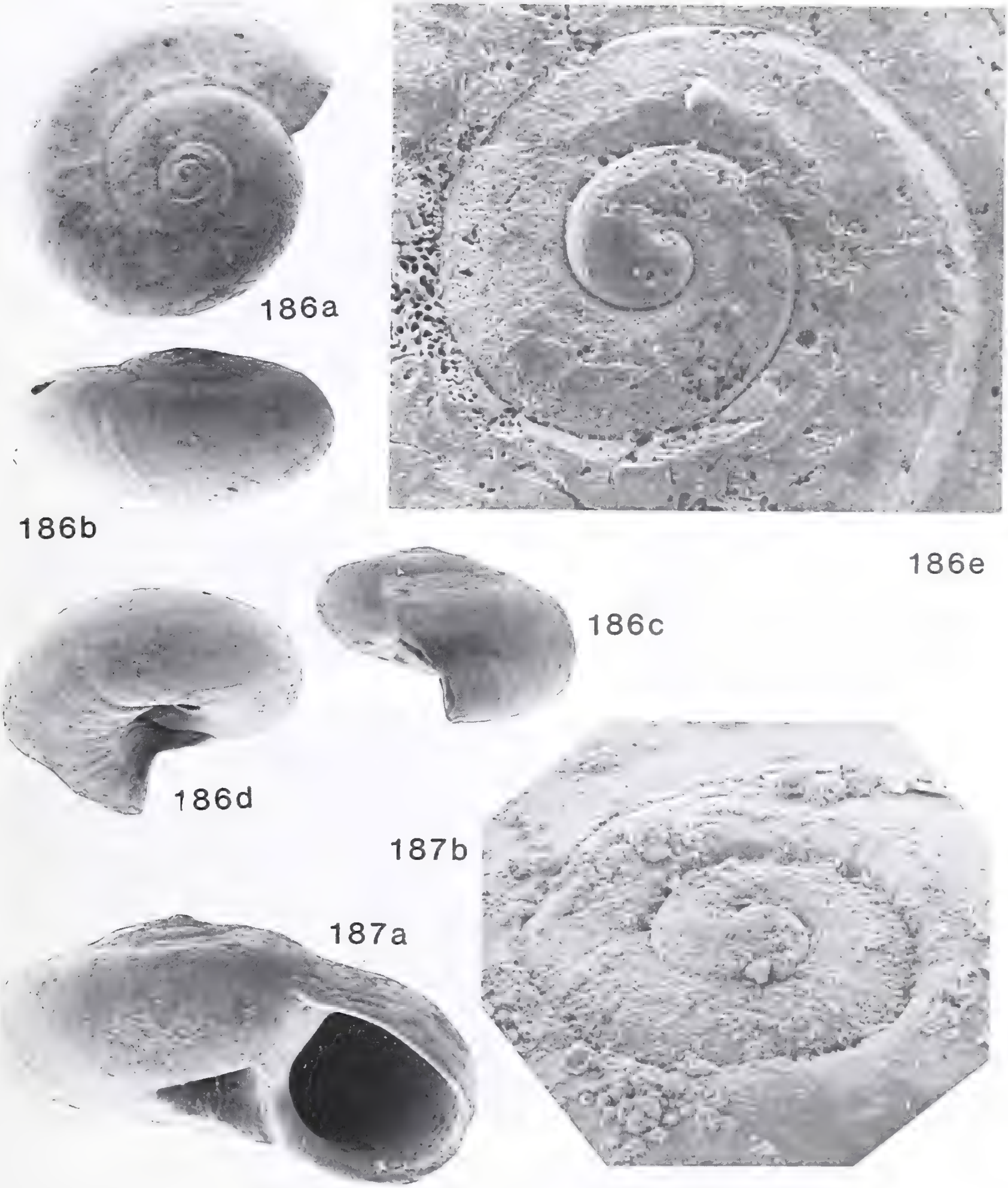
The Pebasian species are fairly similar to *Vitrinella* itself. The discussion below deals briefly first with similar supra-generic taxa, secondly with the nominal genera of Vitrinellidae which the fossils resemble, and concludes with a review of the fossil and living record of similar taxa.

Coahuilix hubbsi (Hydrobiidae, Cochliopinae) was newly described by Taylor (1966: 180, text-figs 8–13) from fresh-water pools in Coahuila Province, northern Mexico. Taylor assigned this single western hemisphere species to his new tribe Horatiini, in which he included the living fresh-water Balkan genera *Horatia* and *Hauffenia*. It is perhaps questionable that such geographically widely-separated genera should be so closely related. However, *Valvata micra micra* and *V. micra nugax*, both of Pilsbry & Ferris (1906: 172–3; pl. 9, figs 7–13) from Texas might well be placed closer to *Coahuilix*, rather than to *Horatia (Hauffenia)* as was suggested by Taylor (1966: 179). Hubricht (1940) recorded but did not figure *Horatia* from Texas and an artesian well in Alabama.

Taylor also suggested (1966: 179) that the three Pebasian species under consideration herein, *Planorbis bourguyi* Roxo (1924: 50, fig. E) from Três Unidos, *Planorbis* sp. of de Greve (1938: 107; pl. 4, figs 29, 30) from Iquitos and the unfigured *Planorbis pebasana* (Conrad, 1874*a*: 30) from either Pichana, Pebas or Old Pebas, were Cochliopinae (Cochliopini) *incertae sedis*. De Greve's specimen is redescribed here. The type material of *P. pebasana* is apparently lost, being absent both from ANSP (Richards 1968) and NYSM (Clarke 1906). Roxo's specimen has not been re-examined by me. He figured only the dorsal view, from which no family assignment is possible. The illustration shows a diameter of 5.2 mm, but the actual size of the specimen is unknown as no scale was given. The suggestion by Parodiz (1969: 166) that *P. pebasana* and *P. bourguyi* might be synonymous cannot be checked.

From Taylor's (1966) description and pen-and-ink type illustrations, it would appear that *Coahuilix hubbsi* (diameter 0.96–1.08 mm) might be distinguished from the similarly-sized *Vitrinella hauxwelli* sp. nov. (p. 226) from Pichana in having only 2¼ as opposed to 3½ whorls. The larger initial hemisphere of *C. hubbsi* has a diameter of about 0.1 mm, as against 0.04 mm in the fossil species. Taylor stated that the embryonic shell of his genus was of one whorl, but gave no description either of its surface or of any changes which separated it from the succeeding teleoconch, other than that the post-embryonic shell was sculptured with raised (collabral) riblets. From the type illustration, these appear to be in addition to the growth lines and are strong enough to make the outline of the shell distinctly rugose in dorsal view. This feature is particularly distinct in the illustrations of Taylor's paratype (1966: figs 12, 13), in which the lower margin of the body whorl also appears to be rugose in front view. The Pebasian fossils lack such riblets. In *C. hubbsi*, European Horatiinae and *V. hauxwelli* the apertures are entire. In mature *C. hubbsi* alone, it is strongly flared: there is no trace of flaring in the similarly-sized *V. hauxwelli*.

The fresh-water basommatophoran Superfamily Glacidorbacea (Ponder 1986: 53) is based on the living Australian *Glacidorbis* Iredale (1943). Ponder at the same time erected *Gondwanorbis* as a subgenus of *Glacidorbis* for the living Chilean species *Glacidorbis magellanicus* Meier-Brook & Smith (1976). This, to date, is the known distribution of the superfamily. *Glacidorbis* and *V. hauxwelli* are of almost identical planorbiform shape and have similar entire apertures. Ponder's description, however, is of a shell which is distinctly larger. *Glacidorbis* attains a diameter of 2.3 mm at 2½ whorls, whilst *V. hauxwelli* has 3½ whorls at a diameter of 1.0 mm. Ponder describes the 'protoconch' of *Glacidorbis* as not being clearly separable from the teleoconch. His illustrations clearly show its granular surface and that the diameter of the initial hemisphere of the shell is about 0.15 mm.

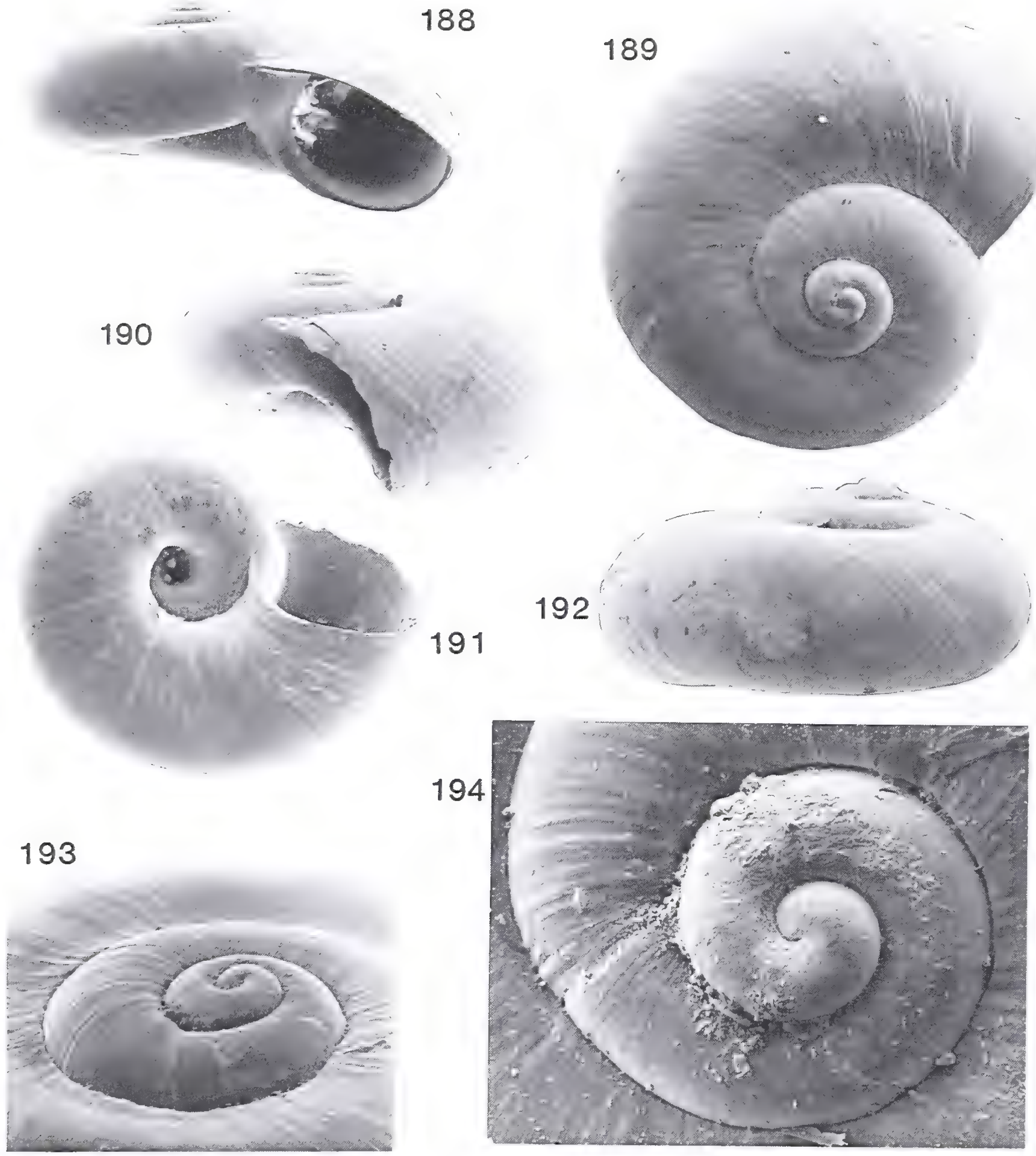


Figs 186–187 *Vitrinella helicoidea* C. B. Adams, type species of *Vitrinella* (s.str.). Recent beach drift; Miami, Florida; presented and identified by D. R. Moore; BMZD 1984240 (2 shells from sample). **186**; a, b, c, d, respectively apical, rear, side and (to show umbilical ridge) obliquely ventral views, all × 25; e, apex, showing aperture of larval shell at about ten o'clock, × 200. **187**; a, front, × 40; b, oblique view of apex showing larval aperture at about eight o'clock, × 200.

The Pebasian fossil material is almost certainly not so well preserved as Ponder's specimens of *Glacidorbis*, but the embryonic shell of *V. hauxwelli* shows no trace of any granular surface. It is much smaller, and is clearly delineated from the teleoconch by a very strong growth line. The growth lines in *Glacidorbis* appear to be virtually orthocline and almost straight, whilst those of the fossils are more prosocline and markedly sinuous.

Vitrinellidae with which the Pebasian fossils should be compared are *Vitrinella* s.str., *V. (Vitrinellops)*, *V. (Striovitrinella)*, *Cochliolepis* and *C. (Tylaxis)*. Doubt must remain about the value of some of the distinctions between these taxa, which seem to be both arbitrary and unnecessary. Neither *Vitrinella* nor its type species were figured in their original descriptions (C. B. Adams 1850). The true identity of *Cochliolepis* is uncertain, as the type specimens of the type species were destroyed. There is no uniformity of opinion as to its correct identification, as the original illustrations (Stimpson 1858) lacked detail.

Vitrinella C. B. Adams (1850: 3) has as type species *Vitrinella helicoidea* C. B. Adams (1850: 9), by subsequent designation of Bush (1897: 122): living, Jamaica, probably



Figs 188–194 *Vitrinella (Vitrinellops) floridana* (Pilsbry & McGinty). Recent; spoil bank of canal SE of Rockport, Texas; presented and determined by D. R. Moore; BMZD 1984241 (7 shells from sample). **188–192**; respectively front, apical, side, basal and rear views, all × 50. **193**; oblique view of apex, followed by rapid expansion in whorl diameter, × 100. **194**; apex with larval aperture at eight o'clock, × 200. (Note, in particular, general similarities in whorl profile between Fig. 193 and Figs 197a, b of *V. (V.) hauxwelli* sp. nov., p. 227).

from beach sand in cove near Port Royal (C. B. Adams 1850: 4). The only specimens available for study are three somewhat worn shells from a beach drift, Miami, Florida (BMZD 1984.240), presented and identified by D. R. Moore (Figs 186, 187). These agree with the description and illustrations in Pilsbry & McGinty (1946: 13; pl. 2, figs 3, 3a, b). The shell has 3–4 whorls in all, and is smooth except for growth lines and a few, apparently random, growth halts. The spire is very low, with an angle of about 150°. Later whorls are rather more convex and the suture lies at the periphery. Growth lines are strongly prosocline and curved, so that the most forward point of the aperture, when viewed from above, lies half-way between the periphery and the suture with the previous whorl. The embryonic shell appears to consist of 1¼–1½ whorls, reaching a diameter of 0.25 mm. Its initial hemisphere appears to be slightly sunken in the spire and has a diameter of about 0.05 mm. The boundary with the teleoconch is marked by a strong growth line, and a rugose ridge almost immediately develops adjacent to the suture on the upper surface of the first teleoconch whorl. The aperture is almost entire except for a slight concavity where it is adpressed to the previous whorl. The inner lip is thickened. The umbilicus is deep and bordered by a well-marked spiral cord.

Vitrinellops was erected as a subgenus of *Vitrinella* by Pilsbry & Olsson (1952: 73). Its type species is *V. zonitoides*

Pilsbry & Olsson (1952: 73; pl. 13, figs 2, 2a, b): Recent, San Miguel Island, Pearl Islands, off the Pacific coast of Panama. They defined their new subgenus as being similar to *Vitrinella* s.str., but lacking the keel bordering the umbilicus. They pointed out (1952: 71) that comparatively few species belonged to *Vitrinella* s.str. (three Pacific species listed, p. 84) whilst the majority (16 Pacific species listed), which could be either smooth or sculptured with minute spiral striae, were assigned to *Vitrinellops*. Their lists were copied by Keen (1971: 373–4). However, *Striovitrinella* (Olsson & McGinty, 1958: 31) was proposed for their newly described striate living Caribbean species, *V. (S.) elegans* (1958: 31; pl. 3, figs 1, 1a–d). The similar Pacific species are now best assigned to this subgenus.

The remarks below on *Vitrinellops* are based on the only good sample of the subgenus available for study. The living *Vitrinella floridana* Pilsbry & McGinty (1946: 16; pl. 2, figs 4, 4a) described from Florida is here reassigned to *Vitrinellops*. Sample BMZD1984241, collected by W. H. Rice from a spoil bank of a canal SE of Rockport, Texas, was specifically determined and presented by D. R. Moore, and contains several well-preserved specimens (Figs 188–194) of 3 – 3½ whorls, with diameter 1.1 – 1.5 mm. The embryonic shell has 1½ – 1¾ whorls with a diameter of about 0.37 mm. In some individuals it is set at a slight angle to the post-embryonic shell. Its initial hemisphere has a diameter of 0.048 – 0.060 mm. Growth lines may be made out on the latter part of the embryonic shell, which is separated from the post-embryonic shell by a very marked, orthocline, growth halt. For a short period the shell then appears to expand more rapidly than the embryonic shell, sometimes giving this stage a rather flared appearance. *V. (Vitrinellops) floridana*, in common with the type species of the subgenus and the majority of the other Pacific species assigned to it by Pilsbry & Olsson (1952), has a low but distinct spire. Only two species dealt with by them approach the planorbiform condition: these are *V. (V.) subquadrata* Carpenter (1856) (1952: 76; pl. 11, figs 5, 5a, b), which has a slightly raised spire, and their own species *V. (V.) margarita* (1952: 74; pl. 13, figs 5, 5a, b), which is planorbiform and was described as having excessively minute spiral striations. This last feature suggests a connection with *Striovitrinella*, whilst its very broad aperture is reminiscent of the otherwise Caribbean–Atlantic *Cochliolepis*. At least one species presently assigned to *Cochliolepis, C. striata* Dall (1889), is spirally striate (see Pilsbry, 1953: 432; pl. 52, fig. 2).

Among the living Pacific species now transferred to *V. (Striovitrinella)* from *V. (Vitrinellops)* is *V. ponceliana* (de Folin 1867), whose syntypes (BMZD 196458, from the Pearl Islands, Pacific coast of Panama) possess an embryonic shell very similar to that of *Vitrinellops*. The post-embryonic shell, which is low-spired with an almost entire aperture and an umbilicus lacking a spiral ridge, differs from typical *Vitrinellops* only in being spirally striate. Although both Pilsbry & Olsson (1952) and Keen (1971) listed the spirally striate and low-spired *Cyclostremella dalli* Bartsch (1911) under *Vitrinellops*, both papers entirely ignored the planispiral, but otherwise very similar, *Cyclostremella californica* Bartsch (1907: 232; pl. 40, figs 10–12). The inclusion of planispiral and almost planispiral species in subgenera of *Vitrinella* suggests that the Pebasian *V. hauxwelli* might also be accommodated within this group.

Among the Pebasian fossils, The single Iquitos shell described by de Greve (1938) as *Planorbis* sp. is the most readily acceptable as a member of the Vitrinellidae, with strong similarities to a number of species normally assigned to *Cochliolepis*. Unlike the apparently more widespread group of *Vitrinella* and its subgenera, the name *Cochliolepis* appears not to have been used for species from the western Pacific, but only for those from the Caribbean and Atlantic. The presence of *V. margarita* suggests, however, that species with *Cochliolepis*-like characters do occur in the Pacific. According to Pilsbry (1953: 433), the type specimen of its type species *Cochliolepis parasitica* Stimpson (1858: 307), collected live from the harbour of Charleston, South Carolina, was destroyed in the Chicago fire of 1871. Pilsbry selected a neotype, USNM 87142, without either describing or figuring it or giving locality details. Pilsbry indicated (1953: 431–3), however, that several authors had misidentified this species, including Gardner (1948: 194; pl. 25, fig. 1). I therefore know of no correctly identified illustration of this species showing its shell characters. Neither the genus nor its subgenus *Tylaxis* is represented in BMZD collections. *Cochliolepis (Tylaxis)* Pilsbry (1953: 434), type species *T. virginica* (Pilsbry 1953: 434; pl. 52, figs 4, 4a, b), Miocene, Virginia, differs from *Cochliolepis* (s.str.) only in having a more thickened columellar and parietal callus and flattened, gently sloping walls of the rather wide umbilicus, and in other, perhaps rather superficial, details.

Typical species of *Cochliolepis* are not unlike *Vitrinellops* except that they tend to be rather large, ranging 2.0 – 6.5 mm in diameter, and are more involute, with the result that the sutures on the upper surface are almost tangential, thus producing a rather flush-sided, low spire. The aperture is entire, or nearly so, and is rather broad. None of the species illustrated in Gardner (1948: pl. 25) nor in Pilsbry (1953: pl. 52) could be confused with the Iquitos fossil. The living *Cochliolepis surinamensis* Altena (1966: 235, figs 2a–d; 1975: 18, figs 8a–d) from a shell ridge near Paramaribo, Surinam, differs from this fossil in that its spire is slightly concave and its aperture not entire, but crescentic, the inner lip strongly embracing the penultimate whorl as in Planorbidae. Furthermore, it seems to be larger at all stages. The holotype has a diameter of 2.7 mm at 2¾ whorls, and from the type illustration the initial hemisphere of the larval shell would appear to have a diameter of 0.08 mm.

The problem whether the new species *V. hauxwelli* from Pichana and *V. degrevei* from Iquitos should be regarded as congeneric cannot be satisfactorily answered for several reasons. The strong growth halt occuring after half a whorl in *V. hauxwelli* is here interpreted as representing the change from embryonic to post-embryonic shell, and would suggest lecithotrophic development, a reasonable assumption as this development type appears to be a common response to reduced salinities in groups whose marine members normally have free-swimming veliger larvae. Unfortunately the single specimen of *V. degrevei* is not sufficiently well preserved to show where its embryonic shell ended. However, in *V. hauxwelli* and *V. degrevei* the initial hemispheres are of similar size and subsequent whorls develop at similar rates, taking account of the fact that the latter species is much more involute than the former. On balance, it seems more likely that one, rather than two similar, genera of marine Vitrinellidae invaded the Pebasian Basin. These fossil species are therefore both assigned, with some reservations, to *Vitrinellops* in spite of the differences in their adult shells, and in spite of the fact that the embryonic shell of *V. hauxwelli* differs so markedly from that of typical marine *Vitrinellops*. Comparisons of Figs 193 and 197a, b, showing their early whorls, clearly demonstrate their general similarity. Disregarding these considerations, however, it could be argued that *V. hauxwelli* belonged to *Vitrinellops* and *V. degrevei* to *Cochliolepis*. But the above discussion on the available genus-group taxa suggests that the boundaries between them are possibly arbitrary, as well as ill-defined, not only because of lack of knowledge of their soft-part anatomy and other biological information, but also because their type-species are not fully understood.

Members of the genera discussed above are mainly tropical in distribution, living on the Pacific coast from California to northern Peru (Pilsbry & Olsson 1945, 1952; Keen 1968, 1971), in the Caribbean (C. B. Adams 1850; Olsson & McGinty 1958), southern United States, including its Atlantic coast (Pilsbry & McGinty 1945–50; Moore 1972) and also the Atlantic coast of South America as far south as Brazil (Altena 1966, 1975; Rios 1985). None of these living species can be confused with the Pebasian fossils.

The same genera occur in Neogene deposits of the south-eastern United States (Gardner 1948; Pilsbry 1953), Venezuela (Weisbord 1962) and Trinidad (Jung 1969). Surprisingly, the rich molluscan faunas from the Canal Zone of Panama, although containing several Vitrinellidae described by Woodring (1957) from the fine-grained sediments of the Gatun Formation, have not yet yielded any similar to those under consideration. No Vitrinellidae have been described from the Neogene deposits of the Pacific coastal strips of Colombia, Ecuador and northern Peru.

Both Gardner (1948: 193) and Woodring (1957: 69) drew attention to the difficulties of vitrinellid classification owing to the paucity of information about living members of the family. Moore (1972) provided a most useful and readable account of the shell morphology and anatomy characteristic of the family, as well as geographical distribution and habitat. He concluded that most vitrinellids were herbivores, with most species living in quite shallow water under rocks, or in grass beds such as those occurring in marine bays and lagoons. All the shells of living vitrinellids that I have been able to examine have embryonic shells characteristic of free-swimming larvae. As far as is known, the present records of the family are the first from a reduced salinity habitat and also the first description of what is interpreted as an embryonic shell of only half a whorl, suggesting lecithotrophic development.

Genus ***VITRINELLA*** C. B. Adams, 1850

TYPE SPECIES. *Vitrinella helicoidea* C. B. Adams (1850: 9). Living, Jamaica; by subsequent designation of Bush (1897: 122).

Subgenus ***VITRINELLOPS*** Pilsbry & Olsson, 1952

TYPE SPECIES. *Vitrinella (Vitrinellops) zonitoides* Pilsbry & Olsson (1952: 73; pl. 13, figs 2, 2a), by original designation.

Vitrinella (Vitrinellops) hauxwelli sp. nov. Figs 195–197

HOLOTYPE. BMPD GG19952, Late Caenozoic, Pebas Beds; Pichana, Peru; Hauxwell Colln, 1870, extracted from matrix, 1980. GG19953–4, GG21516, and GG21517/1–3 (same details as holotype) are paratypes.

NAME. From Juan Hauxwell's collection, purchased by the British Museum in 1870.

DIAGNOSIS. Planorbiform *Vitrinellops* with slightly sunken spire; embryonic shell of half a whorl, terminating with strong growth line; shell smooth except for growth lines; aperture entire, almost circular, but slightly broader than high; sutures very deeply impressed; umbilicus broad.

DESCRIPTION. The shell has three whorls. Adapically, it is almost planispiral, but the minute initial whorl is slightly sunken and deviated. A strong growth line, marking the aperture of the apparently smooth embryonic shell, can be seen in the holotype, and more clearly in paratype GG19953. In both specimens the initial hemisphere has a diameter of 0.04 mm and the maximum diameter of the embryonic shell is 0.08 mm. Close-set growth lines may be seen on the adapical surface of the post-embryonic shell immediately following the embryonic aperture. By the third whorl, the translation rate has increased so that the initial whorl is just visible in side view, except where it is obscured by the last half whorl, whose whorl expansion rate is rather greater than that of earlier whorls. The aperture is nearly circular, slightly wider than high, and is strongly opisthocline, leaning at about 20° from the vertical. The growth lines are clearly visible, slightly sinuous, and fairly regular both in strength and frequency. The umbilicus is deep. The nearly circular form of the aperture, coupled with the rather evolute mode of growth, results in both the upper and lower sutures being deeply impressed.

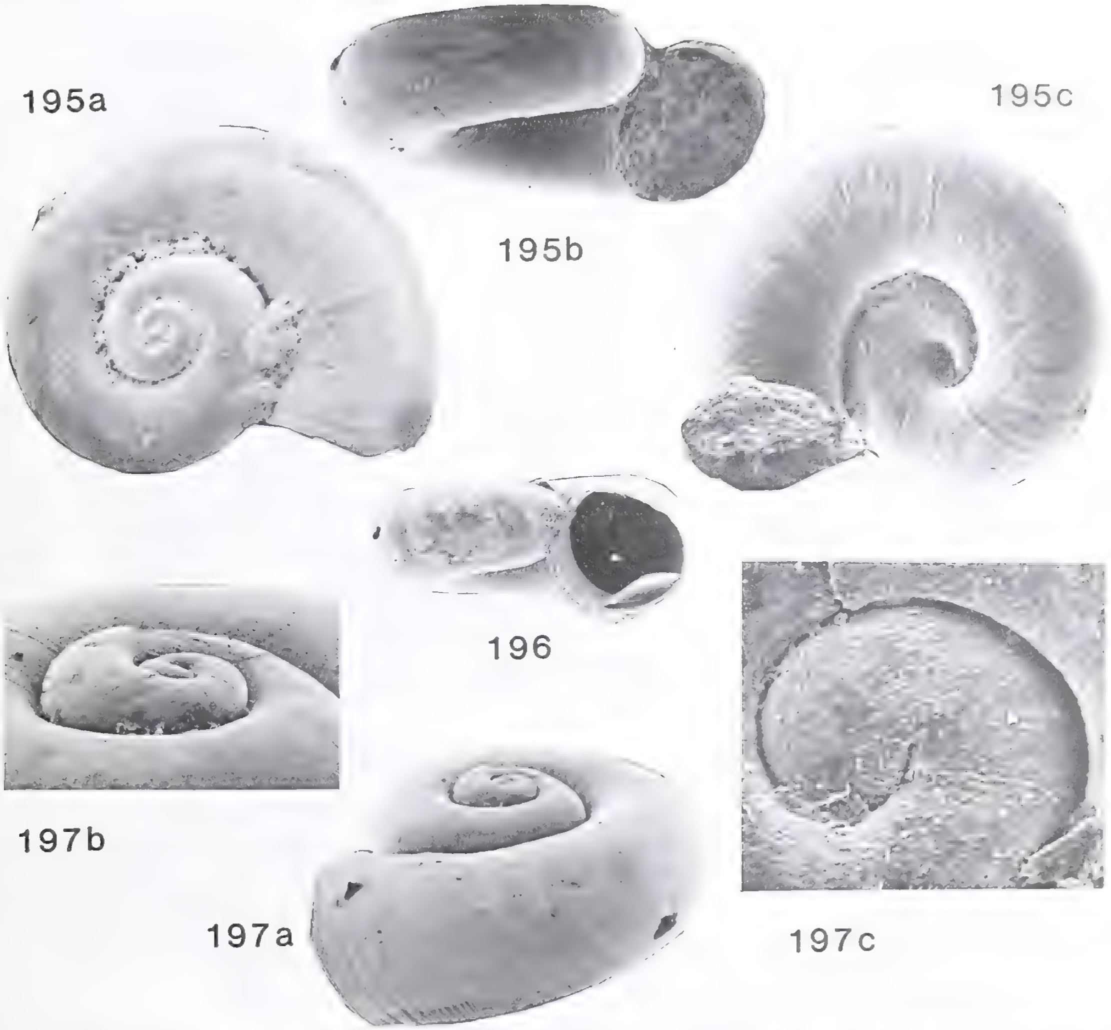
DIMENSIONS. In mm.	d	h	hap	brap
GG19952, holotype, Pichana, (Hauxwell Colln).	1.15	0.57	0.40	0.43
GG19953, paratype.	1.25	–	–	–
GG19554, paratype.	0.85	0.40	0.32	0.35

REMARKS. The half-whorled embryonic shell immediately distinguishes this species from all living *Vitrinellops* which I have examined. Most *Vitrinellops* also have a slightly raised spire. The planorbiform *V. (V.) margarita* Pilsbry & Olsson (1952: 74; pl. 13, figs 5a, b; Recent, Pearl Islands off the Pacific coast of Panama) is larger (d, 2.2 mm) and relatively lower. Its aperture is much broader and is crescentic, embracing the previous whorl. Illustrations (Pilsbry & Olsson 1952: 76; pl. 11, figs 5, 5a, b) show that the planorbiform *V. (V.) subquadrata* Carpenter (1856; Recent, Mazatlan) develops marked columellar and parietal callus by the time it reaches a diameter of 0.85 – 1.0 mm. From above, the growth lines appear to be much more convexly curved than in *V. (V.) hauxwelli*. *Cochliolepis pluscula* Jung (1969: 430; pl. 43, figs 21–23) from the Upper Miocene Melajo Clay of Trinidad might be better referred to *Vitrinellops*. Its rounded aperture is similar to that of the Pebasian species, but it has a distinct spire and a less open umbilicus. It is also slightly larger (d, 1.6 mm).

Vitrinella (Vitrinellops) degrevei sp. nov. Fig. 198

v. 1938 *Planorbis* sp. de Greve: 107; pl. 4, figs 29, 30.

HOLOTYPE. PIMUZ no. 2531. Late Caenozoic, Pebasian; Iquitos, Peru (Peyer Colln). No other material.



Figs 195–197 *Vitrinella (Vitrinellops) hauxwelli* sp. nov. Pebasian; Pichana, Peru; Hauxwell Colln. **195**, **holotype**, GG19952; a, dorsal view; b, front; c, ventral view; all × 50. **196**, paratype, GG19954; front, × 50. **197**, paratype, GG19953; a, slightly oblique side view, × 50; b, view of early whorls, × 120; c, dorsal view of protoconch and first growth lines, × 500. Compare Fig. 193.

NAME. For L. de Greve, who described and figured the specimen in 1938.

DIAGNOSIS. Comparatively large, involute *Vitrinellops* with low spire; adapical surface of whorls weakly convex and sutures only slightly incised; aperture broad; umbilicus narrow.

DESCRIPTION. The unique shell is rather involute in both dorsal and ventral views. There are about 3½ whorls, and in the later growth stages the expansion rate increases slightly. Traces of two rather strong growth halts just prior to the aperture suggest that full size is being reached. The early whorls strongly resemble those of the preceding species in size and shape, but neither growth lines nor a growth halt indicating the transition from embryonic to post-embryonic shell are visible at the half-whorl stage. At 1½ whorls, however, some almost orthocline, slightly forwardly-bowed growth lines can be observed with difficulty, but they are not clear enough to be identified as representing the embryonic aperture. The upper surface of the shell is slightly domed and the sutures of the weakly convex whorls are not deeply impressed. The lower surface is considerably more convex and the umbilicus is narrow: although infilled with immovable matrix, it is unlikely that whorls preceding the body whorl would be visible. The aperture is much broader than high and its periphery is rather below half whorl height. The inner lip is almost straight and vertical, but its upper left portion is slightly indented by the previous whorl. The growth lines are markedly opisthocline, being inclined strongly from the vertical. From above, they appear bowed forward, whilst from below, the bowing is reversed.

DIMENSIONS. In mm.	d	br	hap	brap
Holotype. PIMUZ 2531.	1.93	1.13	0.76	0.90

REMARKS. This species may easily be distinguished from the preceding one by its raised spire and involute form. In shape it somewhat resembles the Recent Surinam *Cochliolepis surinamensis* Altena (1966). The distinctions between the two and the reasons for assigning the fossil to *Vitrinellops* rather than *Cochliolepis* are given above in the remarks on the family (p. 225).

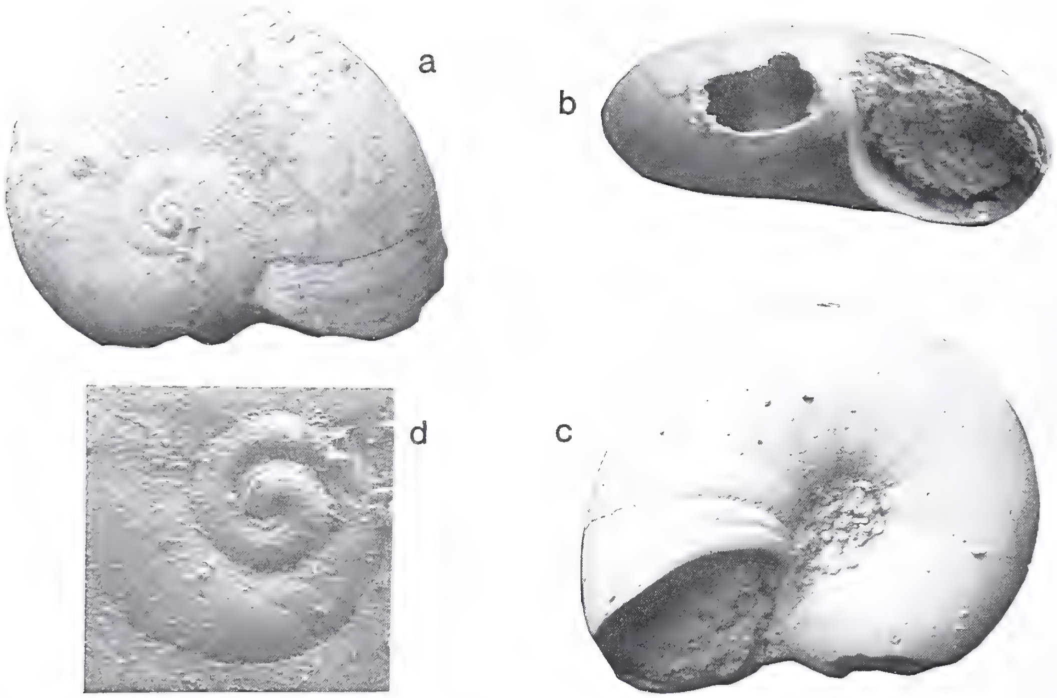


Fig. 198 *Vitrinella (Vitrinellops) degrevei* sp. nov. **Holotype**. Pebasian; Iquitos, Peru; Peyer Colln, PIMUZ no. 2531. a, dorsal view, × 30; b, front, × 30; c, ventral view, showing almost orthocline growth lines, × 30; d, dorsal view of early whorls, × 100.

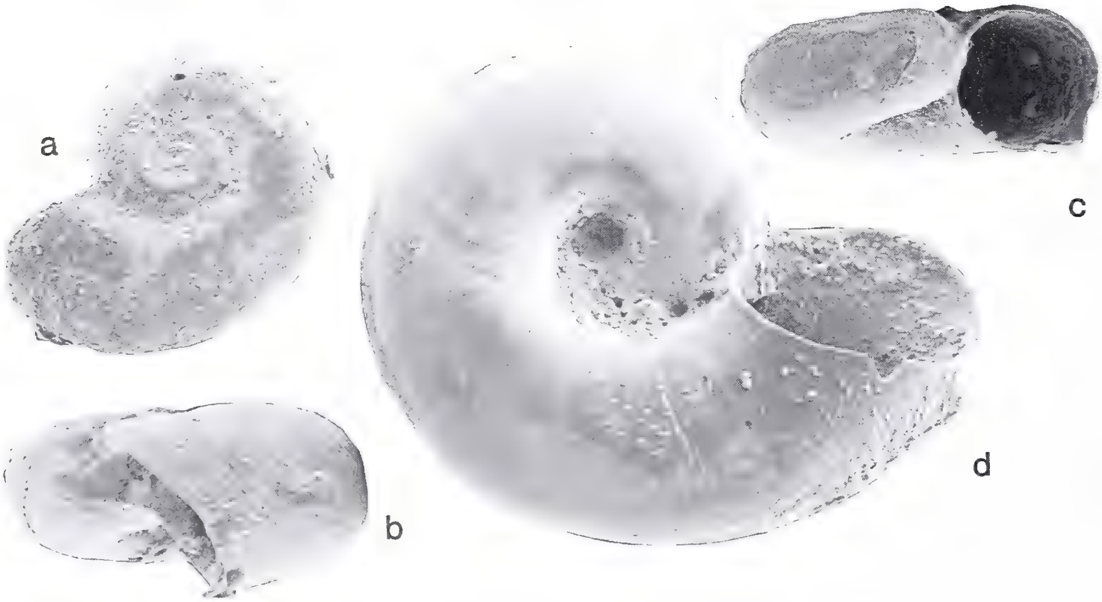


Fig. 199 *Vitrinella (Vitrinellops)* sp. Pebasian; Pichana, Peru; Hauxwell Colln. GG19950; a, dorsal view, × 50; b, side, × 50; c, front, × 50; d, ventral view, showing sigmoid growth lines, × 90.

Vitrinella (Vitrinellops) sp. Fig. 199

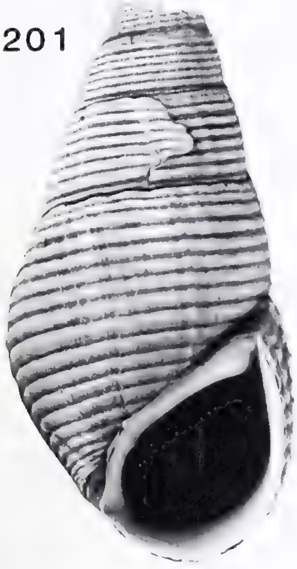
Material. GG19950, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln, 1870, extracted 1980). No further material.

Remarks. This single planorbiform shell, whose upper surface is partly obscured by immovable matrix, does not merit naming as a new species. There are about 2¾ whorls. As far as can be seen, the early whorls are similar to those of the two preceding species. It is, however, clearly separable from the relatively common *V. (V.) hauxwelli* found with it at Pichana by its more involute form, and by the absence of slightly sunken early whorls. Its round aperture, which is similar to that found in *hauxwelli*, immediately distinguishes it from the distinctly spired and involute *V. (V.) degrevei*, which it greatly resembles in ventral view. In dorsal view, the growth lines are very strongly bowed forwards.

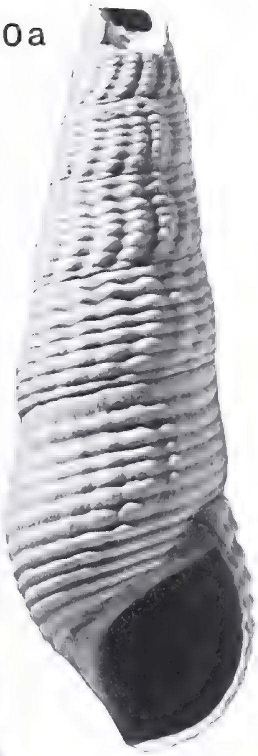
Superfamily **CERITHIACEA** Fleming, 1822

[*nom. transl.* Cossmann, 1906: 1, *ex* Cerithiadae Fleming, 1822: 491.]

201



200a



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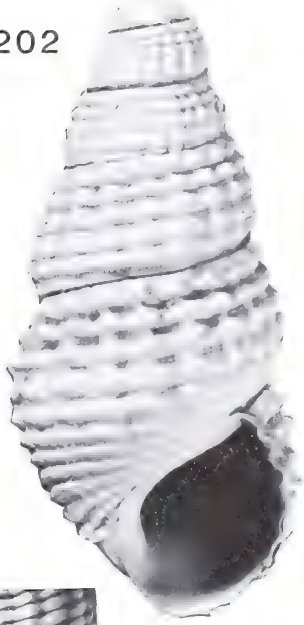

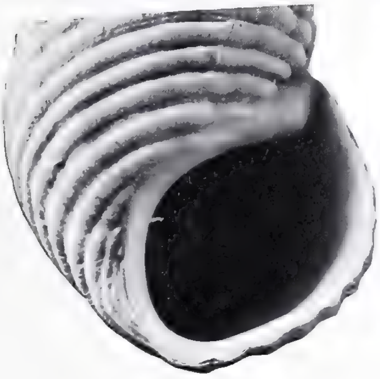

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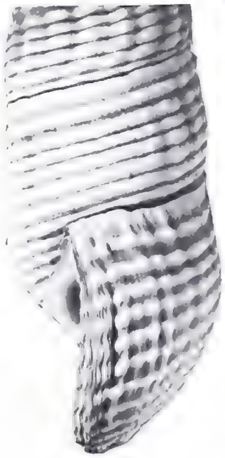


200b

Fig. 200 *Doryssa atra* (Bruguière). BMZD 1984202. Recent; Guyana; Cuming Coll. **Lectotoype** (herein selected) of *Melania nicotiana* Reeve, figured by Reeve (1860: pl. 30, fig. 202). a, front, × 2; b, side, × 2; c, oblique view into aperture, showing growth lines on neck of whorl, × 3.

Fig. 201 *Doryssa consolidata* (Bruguière). BMZD 1984203. Recent; Brazil; Cuming Colln. Specimen figured by Reeve (1860: pl, 1, fig. 3). × 2.

Fig. 202 *Doryssa pernambucensis* (Reeve). BMZD 1984204. Recent; Brazil; Cuming Colln. One of the syntypes of *Melania pernambucensis* Reeve, specimen figured by Reeve (1861: pl. 1, fig. 3). × 2.

Morrison (1954: 357) advanced the supposition that freshwater melanians (i.e. approximately Thiaridae *sensu* Wenz 1939) were polyphyletic, having been derived from several different families of marine Cerithiacea. Although Parodiz (1969) used the families Pleuroceridae and Thiaridae *sensu* Morrison, this classification has not gained general acceptance.

Few palaeontologists would dispute that the Thiaridae (*sensu* Wenz) were almost certainly derived from more than one source, and as Morrison himself pointed out, his work should help in elucidating the zoogeographical story of these snails.

Morrison's classification is followed here, as far as is possible. The Pleuroceridae are dioecious and include *Doryssa* and *Pachychilus*. The Thiaridae dealt with herein are all members of the Hemisininae. They are parthenogenetic and include *Aylacostoma*, *Hemisinus*, *Longiverena*, *Verena* and *Basistoma*, all of which have living type species. The extinct genus *Sheppardiconcha* is also placed in the Hemisininae, on the grounds that it is similar to other members of the family, in particular *Basistoma*.

Morrison's synonymy was accepted by Parodiz (1969: 134; Parodiz *in* Bristow & Parodiz 1982: 43). Because of this controversy, the Pleuroceridae and *Doryssa* are briefly discussed below even though neither appear to be present in the faunas under consideration. Morrison's work is difficult to interpret because of the almost total lack of illustrations and because he names so few species. In discussing *Aylacostoma* (s.str.) he described it as having prominent spiral sculpture, and referred to *Aylacostoma ruginosum* (Morelet) from Central America. This species is spirally striate and has no close resemblance to the comparatively smooth Brazilian type species of *Aylacostoma*. This example, coupled with that of *Doryssa* (below), suggests Morrison's often important and interesting conclusions must always be thoroughly checked. Correct classification of these fossils is not easy when they lack salient diagnostic features such as operculae. The crucially differing modes of reproduction can, in dead specimens, only be revealed by the presence of embryonic shells. Embryonic shells are formed in the parthenogenetic Hemisininae, but, so far, I have not found them in the dioecious Pleuroceridae.

Family **PLEUROCERIDAE** Thiele, 1929

[*emend. et nom. transl.* Morrison, 1954: 357–8, *ex* Pleurocerinae Thiele, 1929: 192 (subfamily)]

Subfamily **PLEUROCERINAE** Thiele, 1929

[*emend.* Morrison, 1954]

Pleurocerinae, *sensu* Morrison, embraces several genera such as *Pachychilus* and *Doryssa* included in Melanatriinae (Thiele 1928: 399) by Thiele (1929: 189) and Wenz (1939: 684–6).

Genus ***DORYSSA*** H. & A. Adams, 1854
(Figs 200–202)

TYPE SPECIES. *Bulimus ater* Bruguière, 1792*a*, Recent, north-western South America. By subsequent designation of Brot (1874: 8).

DIAGNOSIS. Medium to large Thiaridae with spire angle between 20° and 30°; aperture well rounded except for posterior angulation where inner and outer lips meet adapically; neck of body whorl meeting left-most part of inner lip well to the left of shell axis, with lowermost part of shell well to the right of and below that position, where the rounded abapical junction of inner and outer lips occur; lower part of aperture jutting forward strongly; sculpture of spiral ribbing sometimes developing elongate tubercles; opisthocyrt collabral sculptural elements of very variable strength. Operculum circular, multispiral. Dioeceous.

OTHER SPECIES ASSIGNED. Recent: seventeen species (Brot, 1877) including *D. consolidata* (Bruguière) and *D. pernambucensis* (Reeve); additional species described and listed later (von Ihering 1902: 659–665; Pilsbry *in* Baker 1914); all from Atlantic drainage system, Brazil to Venezuela. Fossil: the living *D. devians* Brot, Quaternary, Surinam (Schepman 1887).

DISTRIBUTION. Quaternary and Recent, South America (as above).

REMARKS. It is probable that none of the four fossil species assigned to *Doryssa* by Parodiz (1969) belong to that genus: the only fossil record accepted is given above. *Sheppardiconcha* is herein regarded as a separate genus unrelated to *Doryssa*. *Hemisinus (Basistoma) corrosensis* Pilsbry & Olsson 1935 proves on examination of the holotype (ANSP 13092) to belong to *Hemisinus* (s.lat.) and not, as suggested by Parodiz, to *Doryssa*.

Doryssa atra (Bruguière, 1792) Fig. 200

* 1792*a* *Bulimus ater* Bruguière (*ex* Richard MS): 126.
* 1822 *Melania truncata* Lamarck: 164.
. 1859 *Melania truncata* Lamarck; Chenu: 291, fig. 1989.
*v 1860 *Melania nicotiana* Reeve: pl. 30, fig. 202.
. 1870 *Doryssa atra* (Richard) Brot: 304 (*cum syn.*).
. 1872 *Melania truncata* Lamarck [= *Bulimus ater* Richard]; Brot: 8; pl. 1, fig. 1.
. 1874 *Doryssa atra* (Richard); Brot: 342; pl. 35, fig. 7.
. 1902 *Doryssa atra* (Richard); von Ihering: 661.
. 1939 *Doryssa atra* (Richard); Wenz: 686, fig. 1971.
. 1956 *Melania truncata* Lamarck; Mermod: 66, fig. 127.
. 1956 *Doryssa atra* (Bruguière); Pain: 96, figs 3a–c.
. 1980 *Doryssa atra* (Bruguière); Tillier: 14; pl. 1, fig. 1.

MATERIAL STUDIED. Lectotype (selected herein) of *Melania nicotiana* Reeve, the specimen figured by Reeve (1860: pl. 30, fig. 202) and two accompanying unfigured paralectotypes; Guyana, Cuming Colln, BMZD 1984202.

REMARKS. Tillier (1980) discusses the original collections of Richard and Leblond from which the material named by Bruguière came. Both Brot (1872) and Mermod (1952) examined the Lamarck collection in the Geneva N.H.M. Both *M. truncata* Lamarck and *M. nicotiana* Reeve are synonyms of *D. atra*. The species figured by Reeve (1860: pl. 30, fig. 195) as *Melania atra* Richard was misidentified and subsequently renamed as *Doryssa lamarckiana* by Brot (see Brot, 1874: 344; pl. 35, figs 1, 1a). The species lives in rivers of the Guyanas and north-eastern Brazil (Tillier 1980: 15). The above specific synonymy is not exhaustive.

Family **THIARIDAE** Wenz, 1929

[*emend.* Morrison, 1954: 357–8, 374]

Wenz (1929: 2517) established the Thiaridae as a family. His classification was set out in detail (1939): the family was divided into several subfamilies including Pleurocerinae and Thiarinae (1939: 712). Thiaridae *sensu* Morrison (1954) more or less corresponds with Thiarinae of Wenz (1939).

Subfamily **HEMISININAE** Thiele, 1928

[*nom. transl.* herein, = Semisininae Cossmann, 1909: 125 (subfamily), = Hemisinuseae Thiele, 1928: 401 (tribus), = Hemisinuieae Thiele, 1929: 201 (tribus), = Semisinuinae Wenz, 1929: 2561 (subfamily), = Hemisinuieae Wenz, 1939: 717 (tribus), = Aylacostominae Parodiz, 1969; 141 (subfamily)]

Under Art. 11 (f)(i)(1) of the International Code (ICZN 1985: 25) a family group name must, when first published, be based on the name then valid for a contained genus. This provision is first met by Thiele, 1929. Swainson's (1840) genus was *Hemisinus*. Suprageneric taxa based on the unjustified replacement name *Semisinus* Fischer, 1885 are not valid. Parodiz (1969) based Aylacostominae on Hemisinuieae 'Wenz'. However, in the same work (1969: 143), he used *Hemisinus* Swainson as a subgenus of *Aylacostoma* Spix, 1827, thereby acknowledging that they were not exactly synonymous.

Embryonic shells of up to *c*. 5–6 whorls have been obtained by syringing out the apertures of adult shells of Recent Hemisininae in BMZD dry collections (no spirit material being available). The extent of this study has been severely restricted owing to lack of suitable material. At the most two, but usually only one, embryonic shell has been obtained per adult. Many adults have yielded no embryonic shells, but it is not clear whether this is because none of the soft parts were

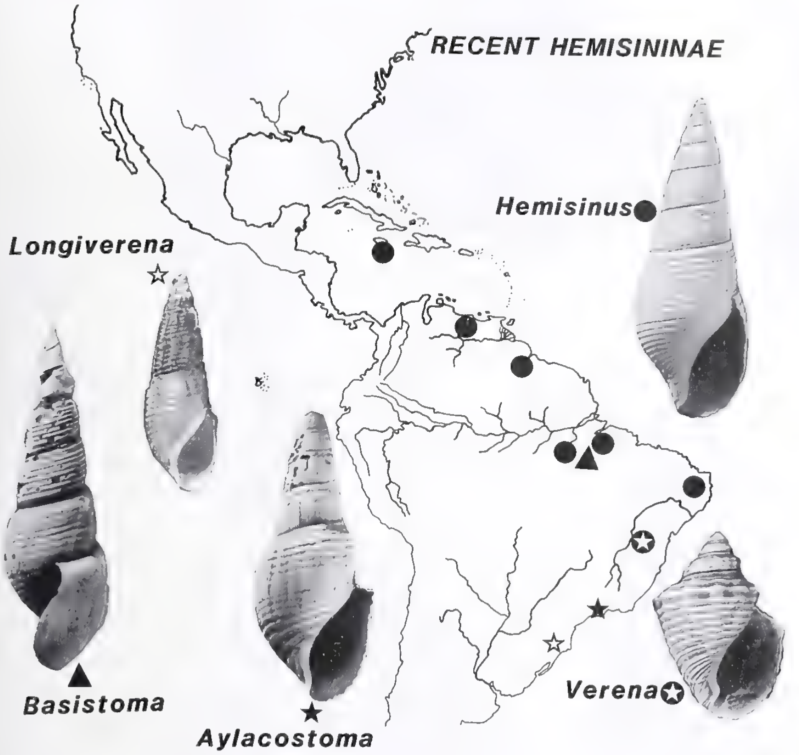


Fig. 203 Recent distribution of Hemisininae: map based on very few authenticated records. ●, *Hemisinus*; ★, *Aylacostoma*; ▲, *Basistoma*; ☆ *Longiverena*; ✪, *Verena*. Inset: *H. brasiliensis* (S. Moricand), × 1; *A. glabrum* Spix, × 1; *B. edwardsi* Lea, × 0.75; *L. tuberculata* (Spix), × 0.75; *V. crenocarina* (S. Moricand), × 0.75; all Brazil.

preserved or whether no embryonic shells were ever present in these particular individuals.

Specimens examined have included representatives of the type species of four genera, *Hemisinus lineolatus* (Wood), *Verena crenocarina* (Moricand), *Longiverena tuberculata* (Spix) and *Basistoma edwardsi* Lea. Embryonic shells of one other living species, *Hemisinus globosus* Reeve, here placed in the synonymy of *H. kochi* (Bernardi), and two young juveniles of fossil *Verena browni* (Etheridge) obtained from washings from the Puerto Nariño deposit have also been studied. All the embryonic shells so far examined have features in common. The shell has a hemispherical, cup-like, origin and is, for the first whorl or so, virtually planorbiform. After this, the whorl translation rate increases rapidly so that the embryonic shell takes on a form increasingly reminiscent of shells mature enough to have enjoyed a free existence. In all the examples studied, the sculpture typical of the early teleoconch soon appears. This varies considerably in the taxa examined. For example, the later embryonic whorls of *H. lineolatus* are virtually smooth, whilst those of *Basistoma edwardsi* are strongly carinate.

Genus *BASISTOMA* Lea, 1852

Type species. *Basistoma edwardsi* Lea, 1852: 296; pl. 30, fig. 1, by original designation. Recent, Rio Tocatins, eastern Brazil. No other assigned species.

Diagnosis. Turritelliform Hemisininae with numerous whorls; spiral sculpture of numerous ribs on early whorls, reducing in strength on later whorls, eventually dying away altogether; no collabral sculpture except strongly reverse sigmoid growth lines giving rise to pronounced sinus at shoulder height or apertural notch; aperture about quarter shell height; outer lip produced forwards below periphery; wide basal notch present; columella weakly callused. Operculum not seen. Embryonic shell with spiral ribbing.

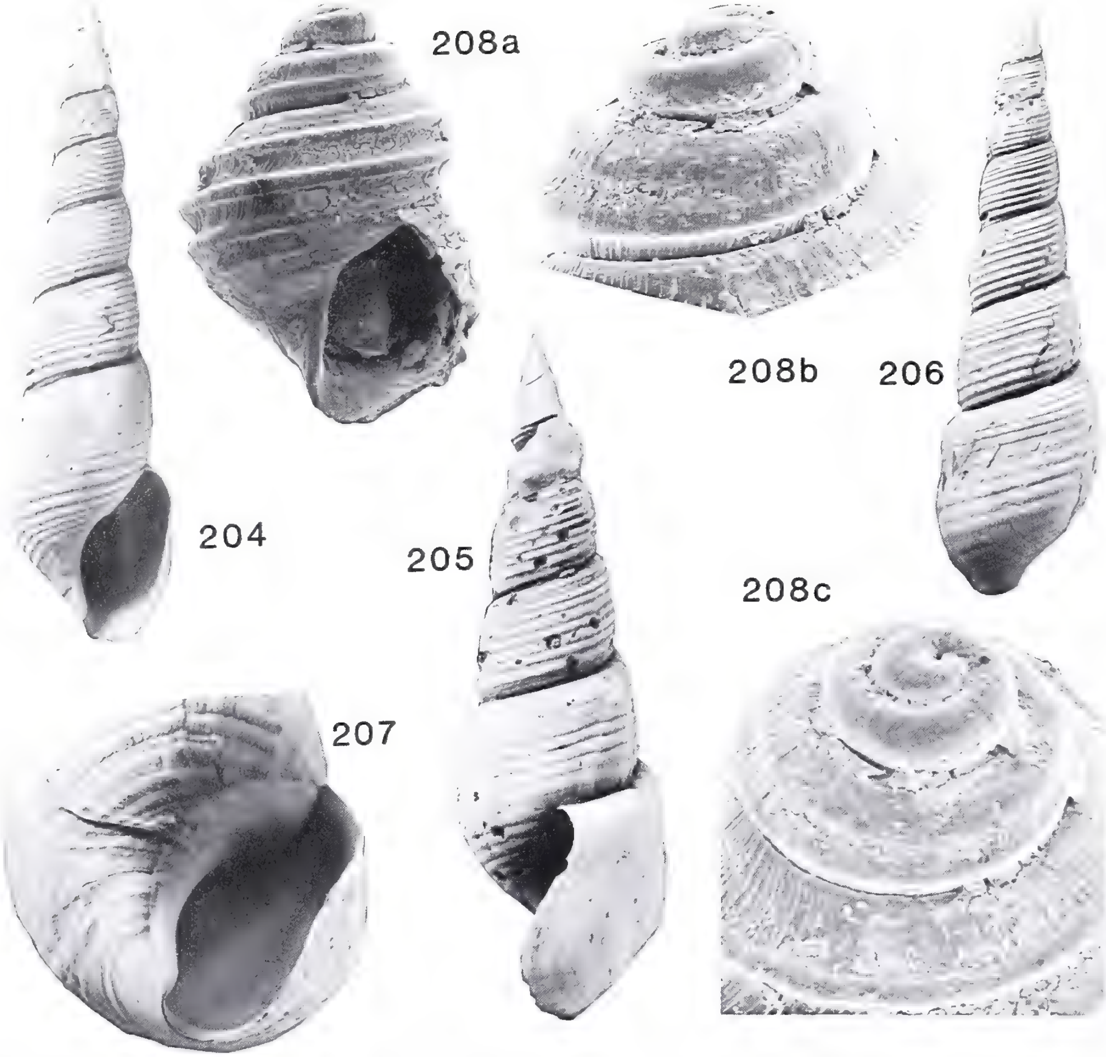
Remarks. The above diagnosis is based on four shells of *B. edwardsi*, one of which yielded an embryo, from Para, Brazil (BMZD). The spires are all eroded. The embryonic shell is spirally ribbed, suggesting that this type of ribbing persists more or less unchanged for the first six whorls or so, before gradually changing into grooves on the later whorls, whilst spiral sculpture becomes obsolete on the last whorl except on the neck region.

No additional information on this taxon is given in later works (Reeve 1860 – *Hemisinus*; Brot 1874: 397; von Ihering 1902: 672). Wenz (1939: 718, fig. 2076) gives the range of *Basistoma* as from the Palaeocene onwards from Europe as well as from south and central America and the West Indies. This pattern of distribution is rejected here. Morrison (1954: 376) wrote that *Basistoma* was the exact equivalent of *Aylacostoma*, being based on the same type of shell. This synonymy is not upheld but helps to explain Morrison's rather broad view of what *Aylacostoma* contained. Comparisons with *Sheppardiconcha* are given under the latter, below.

Genus *SHEPPARDICONCHA* Marshall & Bowles, 1932

Type species. *Sheppardiconcha bibliana* Marshall & Bowles, 1932: 3, by original designation. Miocene, Cuenca Basin, Ecuador.

Diagnosis. Hemisininae resembling *Basistoma*, but with early whorls smooth or sculptured with sharp spiral ribs; sculpture on later whorls variable; spiral sculpture often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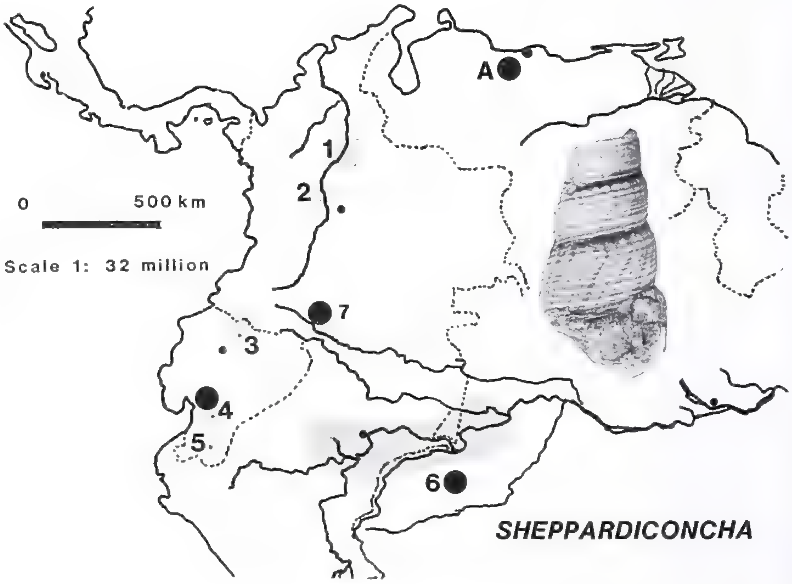
Figs 204–208 *Basistoma edwardsi* Lea. Recent; Para, Brazil. **204**, BMZD 49.1.5.48; front, × 2. **205**, BMZD 49.5.16.13; side, × 2. **206**, BMZD 49.55.16.14; rear, × 2. **207**, BMZD 49.5.16.15; oblique view of aperture and neck of body whorl, × 3. **208**, BMZD 1984205, embryonic shell washed from adult in above sample. a, front, × 25; b, slightly tilted view of early whorls, × 50; c, oblique view of apex, × 50.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SHEPPARDICONCHA

Fig. 209 Distribution of the extinct genus *Sheppardiconcha*. Key as for Fig. 6 (p. 177), with the addition of: A, Siquire Formation, Venezuela (Macsotay 1968). Inset: *S. bibliana* Marshall & Bowles, × 1.25; Miocene; Cuenca Basin, Ecuador.

tuberculate and dominant over collabral; growth lines strongly reverse sigmoid with apex of sinus high on whorl profile; aperture rounded posteriorly, notched below.

OTHER SPECIES ASSIGNED. *Hemisinus tuberculiferus* Conrad, 1874*b*, Late Caenozoic, Pebasian; Iquitos. *Cerithium coronatum* Etheridge, 1879, Late Caenozoic, Pebasian; Canamá, Três Unidos, Iquitos. *Sheppardiconcha lataguensis* sp. nov., Late Caenozoic; La Tagua. *Hemisinus (Sheppardiconcha) picardi* Macsotay, 1968, Miocene, Siquire Formation; northern Venezuela.

DISTRIBUTION. Neogene only; Ecuador, Colombia, Peru, Brazil, Venezuela. Unknown living.

REMARKS. *Sheppardiconcha* and *Basistoma* are compared herein for the first time. The main distinction is the character of the sculpture. *Basistoma* lacks collabral ribbing and its spiral sculpture is simple, bearing no trace either of tubercles or any other modifications. Unfortunately, neither the earliest whorls nor the apertural features of *Sheppardiconcha*, and in particular its type species *S. bibliana*, are sufficiently well known for careful comparisons to be made. It is difficult to assess whether the differences seen between the two genera are really of generic or merely of specific importance.

Marshall & Bowles (1932: 3) suggested that *Hemisinus tuberculiferus* Conrad (1874*b*) also belonged to their new genus *Sheppardiconcha*: this assignment is accepted here.

Morrison (1954: 367) regarded *Sheppardiconcha* as a synonym of *Doryssa* of the Pleuroceridae because of its similar shell characters: this arrangement was followed by Parodiz (1969: 134; *in* Bristow & Parodiz 1982: 43). In poorly preserved or incomplete specimens it is very difficult to separate these two genera belonging to different families. In *Doryssa* the base of the aperture is not notched. Other genera including *Aylacostoma* and *Sheppardiconcha* possess a basal notch. This is seen rarely in the usually damaged specimens of *Sheppardiconcha* (Palmer, *in* Liddle & Palmer 1941: pl. 6, figs 11, 12; *S. bibliana*), and in material of *S. lataguensis*, *S. coronata* and *S. tuberculifera* (PIMUZ) examined herein. As the base of the aperture is frequently damaged, examination of the growth lines on the base of the shell is essential in order to determine whether a basal notch is present. About the last quarter whorl of the outer lip is frequently broken away, and one must orientate the shell by revolving it about its long axis to allow for this.

In practice, the genera may usually be separated by the growth lines, which are strong enough to be clearly interpreted even on many badly damaged specimens. Growth lines in *Sheppardiconcha* are strongly reverse sigmoid with a well-developed sinus or invagination high on the whorl side, at shoulder level, when present. In contrast, those of *Doryssa* are more gently opisthocyrt with the most backward point occuring at about mid-whorl height. In *Aylacostoma* their form is rather like those of *Doryssa*, whilst in *Longiverena* they are somewhat variable in form but never so strongly curved as in *Sheppardiconcha*. In *Longiverena* the collabral sculpture is considerably more important than in *Sheppardiconcha*, whilst *Aylacostoma* is much smoother altogether.

Sheppardiconcha bibliana Marshall & Bowles, 1932

Figs 210–214

* 1932 *Sheppardiconcha bibliana* Marshall & Bowles: 3; pl. 1, fig. 6.

. 1939 *Hemisinus (Sheppardiconcha) bibliana* (Marshall & Bowles) Wenz: 718, fig. 2077.

. 1941 *Hemisinus (Sheppardiconcha) biblianus* (Marshall & Bowles); Palmer, *in* Liddle & Palmer: 400 = 44; pl. 6, figs 1–12.

. 1969 *Doryssa bibliana* (Marshall & Bowles) Parodiz: 134; pl. 15, fig. 12; pl. 16, figs 6, 8, 12.

v 1982 *Doryssa bibliana* (Marshall & Bowles); Bristow & Parodiz: 8, 10, 44, fig. 18.

HOLOTYPE.: USNM 372837, Miocene (given as probably Pliocene, Marshall & Bowles 1932: 2); Biblián, Cuenca Basin (Sheppard Colln). Paratypes are USNM 372838 (several specimens), as above; USNM 372839, Miocene; Paccha, Cuenca Basin (many specimens) (all Sheppard Colln). Type material not studied.

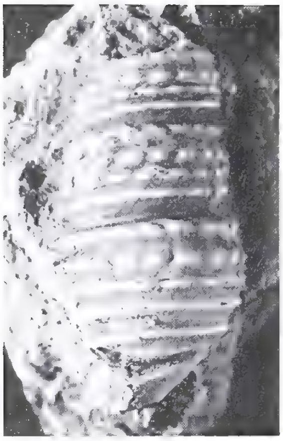
MATERIAL STUDIED. All from Miocene, Cuenca Basin, Ecuador. GG55394–6 (20 specimens) and GG21770–4 from type locality, Biblián (Sheppard Colln); GG19872/1–12, CRB 5; GG19871–6, CRB 8, both top Biblián Formation, near El Valle (Bristow & Parodiz 1982: 8). From the Loyola Formation, numerous specimens including GG19874, GG19875/1–5, CRB 17; GG14364, GG19877/1–10, CRB 14; GG19878/1–2, CRB 2; GG19879/1–5, CRB 28; GG19869, GG19880/1–5, CRB 18; GG19873/1–20, GG21775–6, CRB 61 (see Bristow & Parodiz, 1982: 8, 10, 15 for locality lists).

FURTHER RECORDS. PRI, numerous specimens from several localities, Miocene, Cuenca Basin (Liddle Colln; Olsson Colln) (Liddle & Palmer 1941: 45). CM 46791, Bristow & Parodiz 1982: 44, fig. 18, said to be from the Mangán Formation, Cuenca Basin. Parodiz *in* Bristow & Parodiz (1982: 44) stated that this species is common in BMPD collections from CRB 36a of the Mangán Formation: this may be a clerical error as no specimens of *S. bibliana* from the Mangán Formation are present in BMPD. The specimen figured by Parodiz may have come from the Loyola Formation at CRB 61, a locality from which he did not list the species.

DISTRIBUTION. Miocene, top Biblián Formation, Loyola Formation and ? Mangán Formation, Cuenca Basin, Ecuador (as above).

DIAGNOSIS. *Sheppardiconcha* with apical angle of about 22°; sutures very incised, the adaptical suture channelled; early whorls otherwise straight-sided, later whorls becoming more convex; form of apex unknown; spiral sculpture of about six ribs on succeeding spire whorls, developing into a mixture of broad bands separated by grooves and ribs on later whorls; collabral sculpture of sigmoid growth lines and, on later whorls, low amplitude folds which produce tubercles on adapical spiral ribs.

DESCRIPTION. All the material is damaged. All but two specimens have lost their early whorls and no complete apertures are known. The collections studied suggest that some differential size sorting has occured. At the type locality and CRB 17, the largest shells are less than 25 mm long and 10 mm broad. At other localities most specimens are larger, achieving a maximum length (by reconstruction) of about 50 mm and a breadth of up to 17 mm. A complete specimen of this size would have had about eleven whorls: few have more than five preserved. As the sculpture and whorl profile changes with growth, it appears at first sight that two species might be present. Some specimens with the middle growth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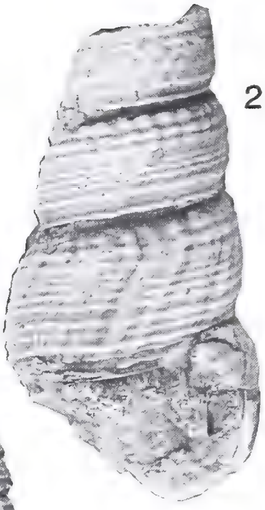
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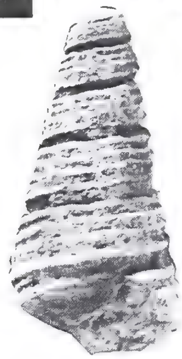
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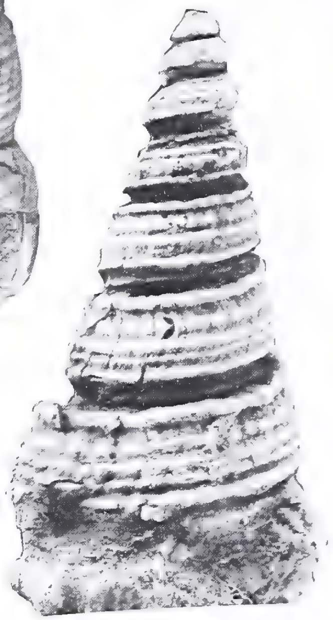
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Figs 210–214 *Sheppardiconcha bibliana* Marshall & Bowles. Miocene; Cuenca Basin, Ecuador. **210–211**, type locality, Biblián, Canar Prov.; Sheppard Colln. **210**, GG21770; × 3. **211**, GG21771; × 3. **212–214**, Loyola Formation, Bristow Colln. **212**, GG19874; Loc. CRB 17, × 4. **213**, GG14364; Loc. CRB 14, × 4. **214**, GG21775; Loc. CRB 61, × 2.5.

stages preserved, however, form the link necessary to show that only one species is present. The earliest whorls appear to be small and biconvex. Their sculpture is not known but the rather simple spiral ribs and sigmoid growth lines typical of the early whorls are present by the third or fourth whorls, and often persist to the seventh whorl, by which a shell height of 20 mm has been attained. Both the spiral and collabral sculpture of later whorls are very variable. A feature in common with the earlier whorls is the tendency for the spiral rib or band nearest the upper suture to be prominent whilst a rather sharp rib is developed just above the lower suture. On the final whorl up to six spiral ribs can be made out with difficulty on a few specimens. The aperture is fairly broad and the callus pad stands proud of the general shell surface.

GG14364 (Fig. 213) from CRB 14, and GG21775 (Fig. 214) from CRB 61, illustrate the two extremes of variation. In GG14364 the whorl profile is very similar to that of young shells from CRB 17. The sutures are rather incised. There are four fairly evenly spaced strong spiral ribs, the uppermost bearing about twenty elongate tubercles per whorl. The other ribs are non-tuberculate. The shell surface is otherwise smooth except for clearly visible growth lines. This specimen is very like *S. tuberculifera* from Iquitos, but the latter has much more angular spiral ribs. In contrast, GG21775 has about ten close-set spiral bands. The uppermost forms a rounded ramp just below the suture and also bears about twenty tubercles on each whorl. The growth lines are bunched to form strong, sinuous rugae.

DIMENSIONS. In mm.	h	br	hap	sa
Holotype, USNM 372837 (from Marshall & Bowles 1932, both text and type illustration)	20	8.5	6	20°
GG21775, CRB 61, Loyola Formation	*26.2 (eh = 39)	12.8	–	21°
GG21776, as above	*31.5 (eh = 43)	16.2	–	–

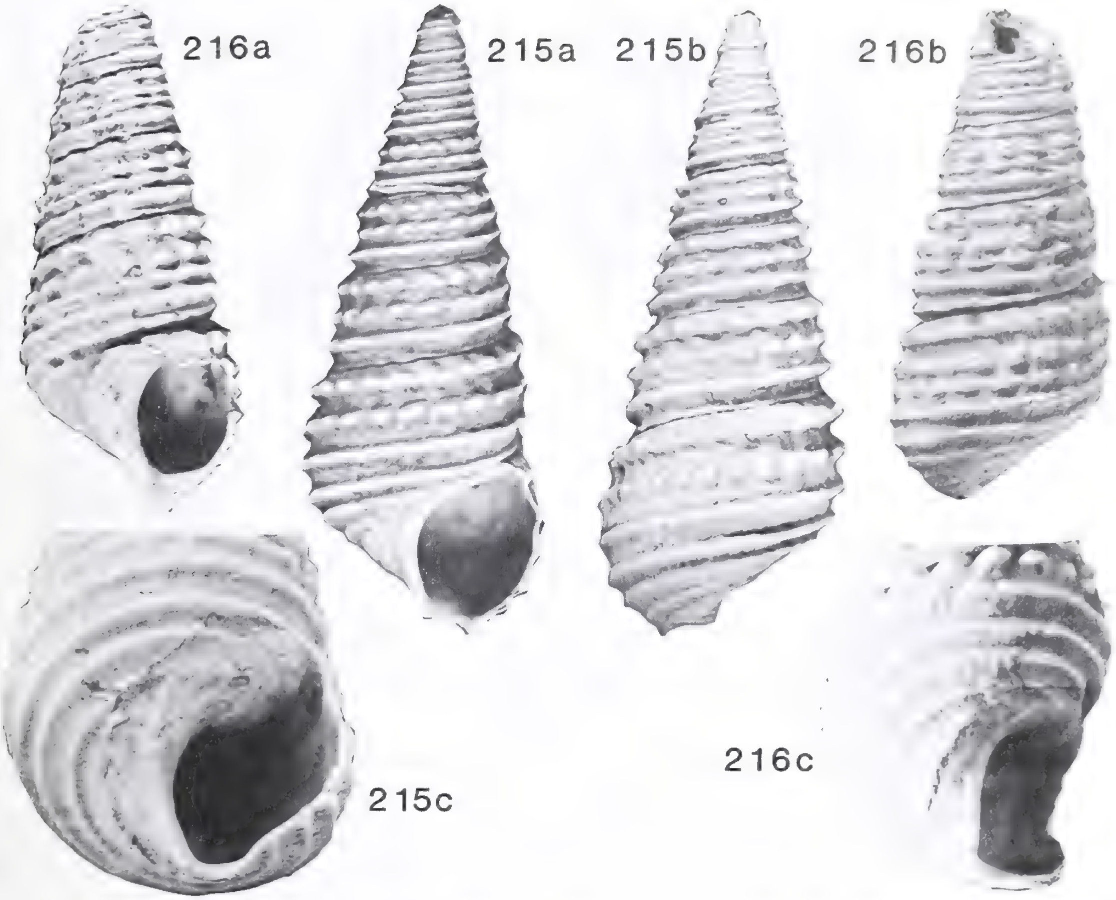
(* = decollated or damaged).

REMARKS. Comparisons with the rather similar *S. lataguensis* sp. nov. are given under the latter, p. 238. *S. bibliana* is easily distinguished from *S. tuberculifera* (Conrad) and *S. coronata* (Etheridge), both of which are essentially smooth except for spiral ribbing bearing strong tubercles. *S. bibliana* is far more common in collections (BMPD, USNM, PRI, and Carnegie Museum, Pittsburgh) than other *Sheppardiconcha*.

Sheppardiconcha tuberculifera (Conrad, 1874*b*)

Figs 215–216

* 1874*b* *Hemisinus tuberculiferus* Conrad: 83; pl. 12, fig. 4.
. 1932 *Sheppardiconcha tuberculifera* (Conrad) Marshall & Bowles: 3.
v 1938 *Semisinus tuberculiferus* (Conrad) de Greve: 104; pl. 4, figs 1–6, 12.
. 1966 *Hemisinus (Sheppardiconcha) tuberculiferus* (Conrad); Willard: 66–68; pl. 63, figs 6–8.



Figs 215–216 *Sheppardiconcha tuberculifera* (Conrad). Pebasian; Iquitos, Peru; Peyer Colln. **215**, PIMUZ 330; figured by de Greve (1938: pl. 4, fig. 1). a, front, × 4; b, back, × 4; c, aperture and neck of body whorl obliquely from below, showing anterior notch, × 6. **216**, PIMUZ 351; figured by de Greve (1938: pl. 4, fig. 12). a, b, c, same views and magnifications.

. 1969 *Aylacostoma (Hemisinus) tuberculifera* (Conrad) Parodiz: 143.

Type material. ANSP, Late Caenozoic; Iquitos (Conrad 1874*b*) (not seen).

Material studied. PIMUZ 330, figured by de Greve, 1938: pl. 4, fig. 1; PIMUZ 351, de Greve, 1938: pl. 4, fig. 12; Late Caenozoic, Iquitos.

Further occurences. All late Caenozoic. Negro Urca, 200 km NW from Iquitos (Willard 1944: 66); Rumi Tuni Valley of Napo River, 225 km north from Iquitos (Willard 1944: 67, 68).

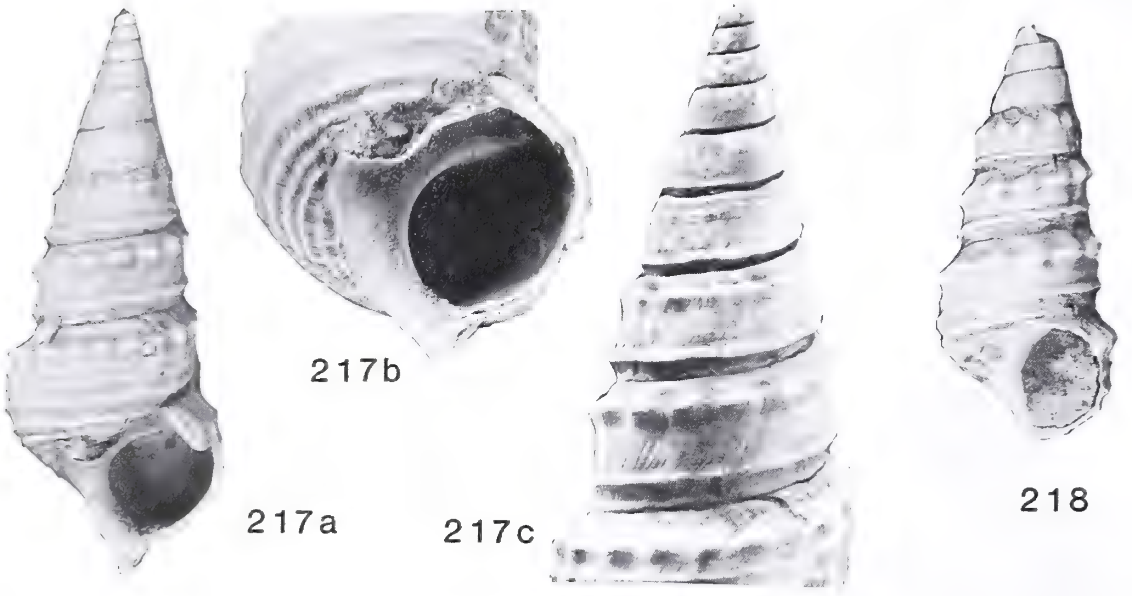
Distribution. Late Caenozoic, Pebasian; Iquitos and district, Peru (as above).

Diagnosis. *Sheppardiconcha* with 3–5 angular spiral ribs on spire whorls; upper spiral ribs strongly tuberculate, lower ones less so; collabral ribbing absent.

Description. The apex is not preserved in any of the specimens examined. If complete, adult shells would have had about twelve whorls. PIMUZ 330 has a damaged apex and a total of nine whorls preserved. The first three of these are undoubtedly post-nuclear. They are pagodiform, with a definite carina developed not far above the lower suture. By the third whorl present, two further spiral ribs have appeared on the ramp, above the carina. On the following whorl, the first sign of tuberculation manifests itself as irregular interruptions of the spiral ribbing. By the fifth or sixth whorl present, the adult sculpture is fully developed. It consists of 7 – 12 spirally elongate tubercles per whorl on the upper two spiral ribs, whilst the lower rib (the continuation of the original carina) is intermittently constricted and almost tuberculate. A fourth smooth rib marks the lower suture on these later whorls. The sculpture of PIMUZ 351 differs mainly in that there are five spiral ribs, the upper three being tuberculate. In addition, the lowest spiral rib gradually moves upwards away from the lower suture as growth proceeds, with the result that the form of the suture is inconstant. On the neck of the body whorl there are either three or four spiral ribs. In this species the collabral sculptural elements consist of the basically spiral tuberculations, which however are arranged collabrally, and also the strongly opithocyrt growth lines.

Dimensions. In mm.	h	br	sa
PIMUZ 330	20.8	8.3	27°
PIMUZ 351	16.4	7.3	24°
PIMUZ 348 (from de Greve 1938: 104)	33.9	11.6	28
Type illustration (from Conrad, 1874*b*: pl. 11, fig. 4)	–	–	26°

Note. Conrad gave no scale. His illustration was 38 mm high and was of a front view. Pilsbry (1944) stated that his specimen was 35 mm high; his figure was of a back view.



Figs 217–218 *Sheppardiconcha coronata* (Etheridge). Pebasian; Canamá, Peru; Barrington Brown Colln. **217**, GG21223 (*ex* 97722); **lectotype** (herein selected), figured by Etheridge (1879: pl. 7, fig. 5). a, shell with broken outer lip, orientated almost in side view, × 2.5; b, aperture obliquely from below, × 4; c, early spire whorls, × 4. **218**, GG21224; paralectotype, front view, × 2.5.

REMARKS. No lectotype selection is made because, without studying the relevant material, there is no way of telling whether Conrad (1874*b*) and Pilsbry (1944) figured the same specimen or not: Conrad (1874*b*: 82) had stated that the species occurred crowded in the clay. No detailed diagnosis and description is given here either, as only two shells were studied, to decide on the generic determination and to compare with *S. coronata* (Etheridge). Conrad (1874*b*: 82) gave the type locality as 'Iquitos, about 100 miles West of Pebas'. This locality was misquoted as 'Pebas' by both Pilsbry (1944) and Parodiz (1969); there are no other records of the species from Pebas. Conrad's illustration is probably partly a reconstruction for he stated (1874*b*: 83) that the labrum was broken in every specimen. In contrast, the aperture he illustrates appears to be undamaged.

S. tuberculifera is similar to *S. coronata* (Etheridge) in enough features to suggest a fairly close relationship. The ribbing of both consists of rather sharp angular spiral carinae. In addition, in *S. tuberculifera* there are 3 – 5 spiral ribs on later whorls and all but the most abapical bear tubercles very similar to those present on *S. coronata*. However, the early whorls of *S. tuberculifera* are pagodiform, not straight-sided: they bear two, and later three, spiral ribs, the lowest of which forms the carina. However, the pagodiform early whorls of *S. tuberculifera* serve to distinguish it from *S. coronata*, whose early whorls are straight-sided. In *S. bibliana* the early whorls have strongly incised sutures, whilst the central part of the whorl is straight-sided.

Sheppardiconcha coronata (Etheridge, 1879)

Figs 217–218

*v 1879 *Cerithium coronatum* Etheridge: 87; pl. 7, fig. 5.
. 1924 *Cerithium coronatum* Etheridge; Roxo: 46.
. 1938 *Cerithium(?) coronatum* Etheridge; de Greve: 106; pl. 3, figs 13–16, 20.
. 1967 *Aylacostoma (Longiverena) coronatum* (Etheridge) Santos & Castro: 413, figs 4–6.
1981 *Aylacostoma (Longiverena) coronatum* (Etheridge); Costa: 645; pl. 1, figs 13–14.

LECTOTYPE (selected herein). GG21223, specimen described and figured by Etheridge (1879); Late Caenozoic, Pebasian; Canamá, Brazil (Barrington Brown Colln). GG21224, as above (not figured by Etheridge) is a paralectotype.

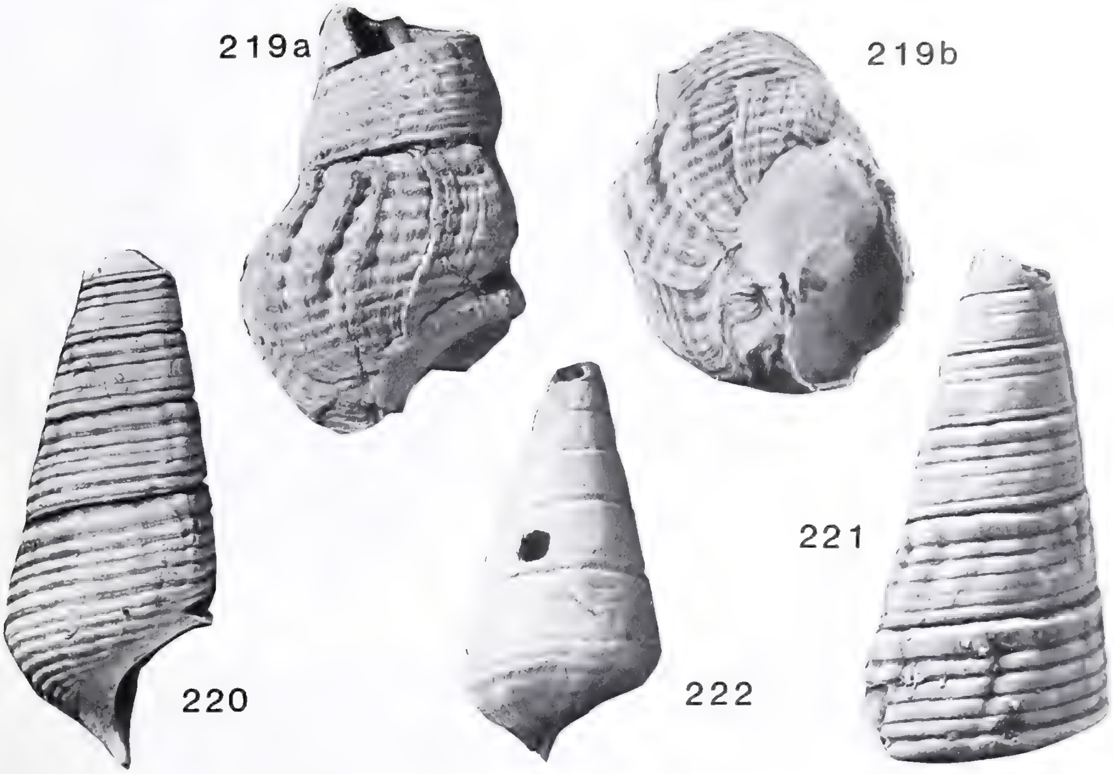
FURTHER MATERIAL STUDIED. GG21511, Canamá, juvenile shell extracted from matrix of Barrington Brown Colln in 1984.

FURTHER OCCURRENCES. Late Caenozoic: Três Unidos, Brazil (Roxo 1924, Santos & Castro 1967, Costa 1981); Iquitos, Peru (de Greve 1938).

DISTRIBUTION. Late Caenozoic, Pebasian; Upper Amazon Basin, Brazil and Peru.

DIAGNOSIS. Small acute-spired *Sheppardiconcha* with apical angle of about 30°; early whorls smooth, straight-sided with incised sutures; later whorls bicarinate; one or two spiral ribs developed between carinae on last whorl or so; body whorl with up to eight spiral ribs below periphery; collabral sculpture, confined to last three whorls, of folds producing coronate shoulder and dying out on flank of whorl.

DESCRIPTION. The apex is unknown, but examination of the lectotype – on which ten whorls are present – shows that the earliest whorls would have been very small. The first four preserved whorls are very weakly convex. They are virtually unsculptured, but the presence of strongly opisthocyrt growth lines shows that they are well preserved and not worn smooth. A carina is developed low down on the fourth whorl, making the suture incised and the flank of the whorl increasingly straight-sided. Two whorls later the second carina develops at the shoulder, and within a further whorl becomes coronate. Two or three extra, rather angular, spiral ribs are developed between the two carinae. On the final whorl up to eight spiral ribs are developed below the periphery, the rib



Figs 219–222 *Sheppardiconcha lataguensis* sp. nov. Late Caenozoic; 1.5 km upstream from La Tagua, Colombia; Weeda colln. **219**, GG19856, **holotype**. a, orientated with broken aperture facing front, × 3; b, obliquely from below, showing aperture and growth lines on neck region of body whorl, × 3. **220**, GG19857, paratype, orientation same as Fig. 219a, × 3. **221**, GG19858, paratype, × 3. **222**, GG19859, paratype, × 8.

lying in line with the adapical suture being particularly strong. The collabral sculpture is confined to later whorls only and consists of 12 – 20 folds per whorl. These are strongest at the shoulder where they form the coronae, and die out both above on the ramp and below on the flank of the whorl, sometimes just affecting the lower carina. The outer lips are broken in both specimens. The inner lip on the lectotype is callused from the base of the columella upwards but is broken away in the parietal region. The callus is arched away from the surface of the columella, leaving a space between the two. The growth lines show no sign of a basal apertural notch.

DIMENSIONS. In mm.	h	br	h/br	sa
GG21223, lectotype, Canamá.	29.5	11.5	2.57	29°
GG21224, paralectotype, Canamá.	20.8	9.7	–	27°
de Greve 1938, Iquitos.	27.4 (max)	–	–	28°–32°
Santos & Castro 1967, Três Unidos.	29 (max)	–	–	23°–30°
Costa 1981, Três Unidos.	33	–	–	27°

Note. Dimensions from de Greve, Santos & Castro and Costa taken from their text, except for spire angles, which are taken from their illustrations.

REMARKS. This species is fairly close to *S. tuberculifera* (Conrad), with which it occurs at Iquitos, and also to *S. lataguensis* sp. nov. (below). Comparisons are given under these species.

Sheppardiconcha lataguensis sp. nov. Figs 219–222

HOLOTYPE. GG19856, 1.5 km upstream from La Tagua (Weeda Colln). GG19857–9 and GG19885–6, information as above, are paratypes.

NAME. From locality of La Tagua.

DIAGNOSIS. Moderate-sized with little or no collabral sculpture; early whorls smooth; sculpture on later whorls consisting of 5–7 increasingly strong spiral grooves separated by broad, flat-topped interspaces; sutures incised; whorls almost straight-sided, but becoming biconvex on last whorl or so.

DESCRIPTION. All the specimens are broken. Undamaged apices and apertures are unknown, and the narrowest whorl preserved has a diameter of about 1 mm. Fully grown shells would have had 12–14 post-apical whorls and the total height is estimated as about 45 mm. Traces of spiral sculpture first appear on the third whorl present and consist of a shelf-like rib just above the incised lower suture; after about the eighth whorl this loses its relative prominence, merging into the general sculptural pattern. A very weak spiral groove may sometimes be seen at about mid-height of the third whorl; other grooves are soon added so that the full complement of five or six, but rarely seven, are present by the sixth whorl, reaching about full strength three whorls later. On the penultimate and final whorls the grooves become nearly as broad as the intervening ribs. Collabral sculpture is absent except for very weak and irregular folds. The growth lines are strongly curved and a combination of opisthocline–opisthocyrt. On the last whorl or so, there may be growth halts, giving a rugose appearance. The full growth lines are seen on

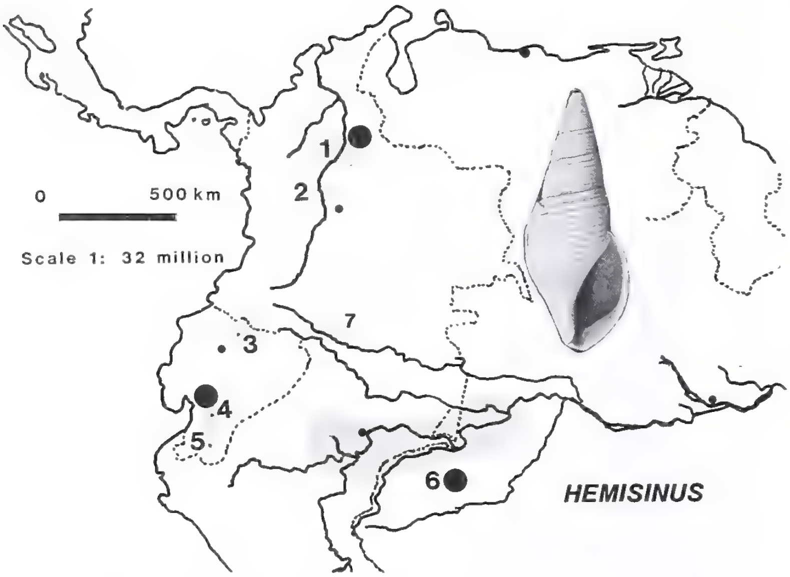


Fig. 223 Tertiary distribution of *Hemisinus*. Key as for Fig. 6 (p. 177). Inset: *H. sulcatus* Conrad, × 1.25; Pichana, Peru.

the last whorl: they are reverse sigmoid and strongly recurved at the base, indicating that the outer lip and basal notch would have had a typical *Sheppardiconcha* shape in unbroken specimens. The inner lip is not strongly callused even in fully grown shells. The earlier whorls are very straight-sided, with the apical angle between 20° and 24°; they form an acute cone, broken only by the slightly incised suture and the rather swollen bands adjacent to it. The last two whorls, however, are increasingly biconvex, with the periphery fairly low down.

DIMENSIONS. In mm.	h	eh	br	sa
Holotype, GG19856	19.0	45	13.5	–
Paratype, GG19857	22.1	30	9.7	21°

(Both specimens decollated and otherwise damaged)

REMARKS. This species is distinguished from other fossil *Sheppardiconcha* by the almost complete lack of collabral sculpture. *S. bibliana* Marshall & Bowles is fairly similar, having a last whorl more convex than the preceding ones and sculpture mainly of spiral grooving. However, its whorls are always less straight-sided and the sutures more impressed. Its spiral grooves are more numerous and less regularly spaced, and it always has some collabral folding. *S. coronata* (Etheridge), like *S. lataguensis*, has smooth, straight-sided early whorls; it is easily distinguished by its later whorls which bear sculpture of sharp spiral ribs, the one on the shoulder being strongly coronate.

The northern Venezuelan Miocene species originally described as *Hemisinus (Sheppardiconcha) picardi* Macsotay (1968: 302; pl. 1, figs 1, 5, 8) is similar to *S. lataguensis* in having predominantly spiral sculpture. It may be distinguished from the latter by its strong subsutural cord.

Genus ***HEMISINUS*** Swainson, 1840

[= *Semisinus* Fischer, 1885: 701, unjustified emendment of *Hemisinus* Swainson, 1840: 199, 341]

TYPE SPECIES. *Melania lineolata* Wood, 1828: 42; = *Hemisinus buccinoides* Reeve, 1860: pl. 1, fig. 3. Recent, Jamaica. By monotypy.

DIAGNOSIS. Relatively high-spired Thiaridae with aperture about two-fifths shell height; columella separated from outer lip by anterior notch; shell smooth or with weak spiral sculpture; collabral sculpture absent; whorls weakly convex, nearly straight-sided, lacking ramp and shoulder; operculum rapidly expanding, paucispiral, auriculate.

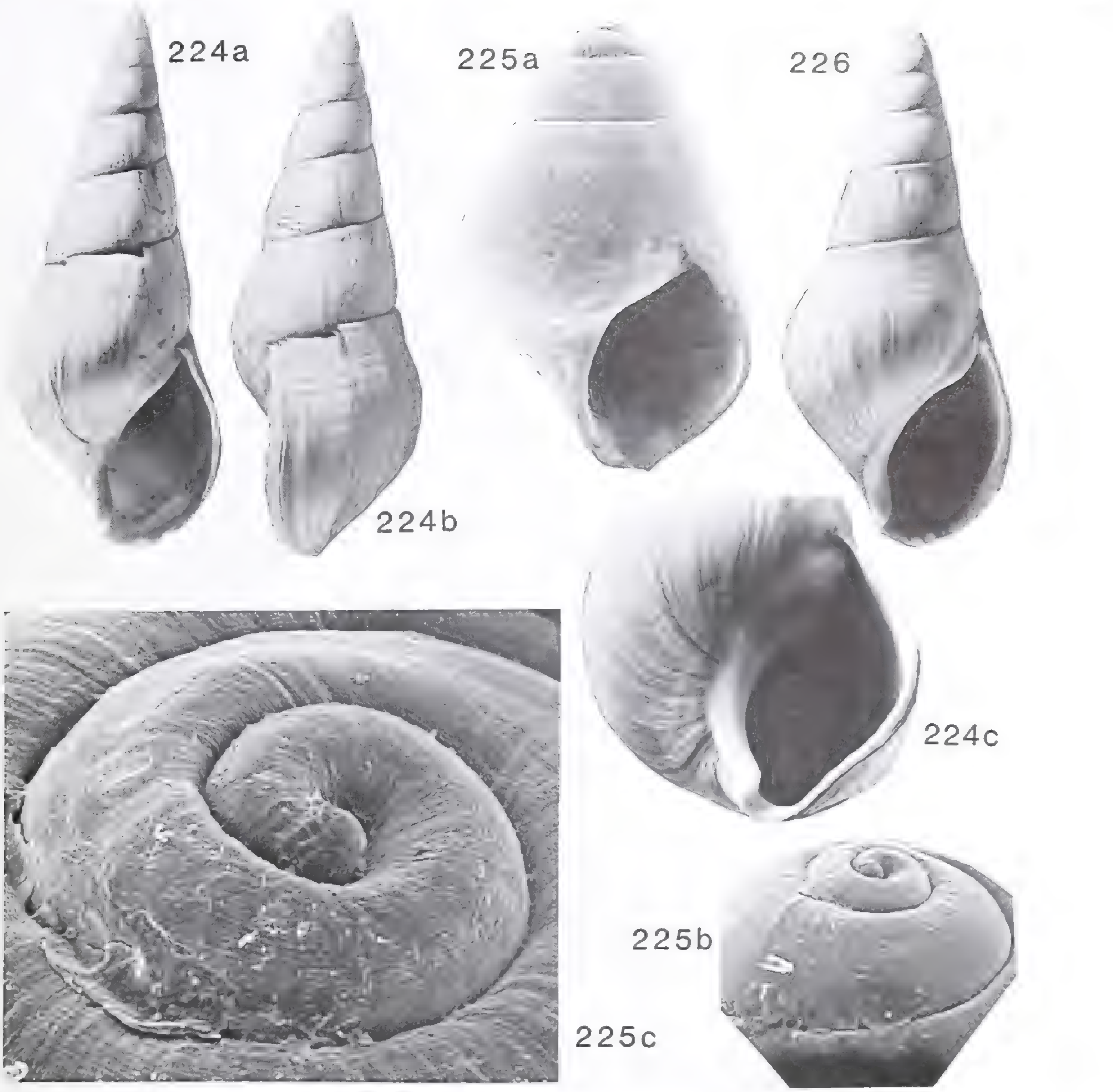
SPECIES ASSIGNED. Fossil: *Hemisinus corrosensis* Pilsbry & Olsson, 1935; Tertiary, Los Corros Formation; Colombia. *Hemisinus sigmachilus* Pilsbry & Olsson, 1935; Tertiary, Mugrosa Formation; Colombia. *Hemisinus* sp. indet., = *H. sulcatus* Parodiz *in* Bristow & Parodiz, 1982: 47 (*pars*), *non* Conrad; Miocene, Mangán Formation; Ecuador (see p. 246). For *Hemisinus sulcatus* Conrad, 1871*b*; Pebasian; Pichana, Peru, see under *H. brasiliensis* (Moricand, 1838) (p. 244). For *H. sulcatus* de Greve, 1938; Pebasian; Iquitos, see under *H. kochi* Bernardi, 1856 (p. 240).

Recent: Several species from northeastern South America and the Caribbean, described in monographs by Reeve (1860) and Brot (1878) are assigned to *Hemisinus*. Some species described from other parts of South America and elsewhere do not appear to be congeneric.

DISTRIBUTION. ? Palaeogene, Neogene and Recent northern and eastern South America and Caribbean.

REMARKS. The evidence (Pilsbry & Olsson 1935, Wheeler 1935) for the Los Corros and Mugrosa Formations being Eocene and Oligocene respectively is far from conclusive and is discussed in the section dealing with the Magdalena Valley, p. 333. The fossil occurences of living species described below are, however, definitely in Neogene strata. Many of the nominal living species are based on small and often poorly localized samples: a thorough taxonomic study would almost certainly reduce their number considerably.

Neither *Melanella karsteni* Anderson, 1928 (Fig. 447, p. 335) from the Tertiary of Colombia, tentatively placed in *Hemisinus* by Pilsbry & Olsson (1935: 12), nor *H. gracillimus* Pilsbry & Olsson 1935 from the La Cira Formation of



Figs 224–226 *Hemisinus lineolatus* (Wood). Recent, ? Caribbean only. **224**, BMZD 1984206; **lectotype** (herein selected) of *Strombus lineolatus* Wood, figured by Wood (1828: pl. 4 [*Strombus*], fig. 11) and by Gray (1834: pl. 13, fig. 4); locality unknown; Gray Colln. a, front, × 2; b, side, × 2; c, aperture and neck of body whorl obliquely from below, × 3. **225**, embryonic shell syringed out of adult, unlocalized, dried specimen of *H. lineolatus*, BMZD 1984207; a, front, × 15; b, oblique view of apex, × 15; c, apex, × 200. **226**, BMZD 1984208; holotype of *Hemisinus buccinoides* Reeve, figured by Reeve (1860: pl. 1, fig. 3), labelled 'Jamaica?'; Cuming Colln; front, × 2.

Colombia, nor *H. pictus* Pilsbry, 1944, from the supposed Oligocene of the Pachitea River, Peru, are well enough preserved for generic assignment. The last, as Pilsbry pointed out, has spirally arranged dashes of colour characteristic of *Hemisinus*.

Gray (*in* Griffith & Pidgeon 1834: 598) is frequently credited with authoriship of *Melania lineolata*, but Wood's earlier work, in which the species is figured, is clearly valid.

Hemisinus lineolatus (Wood, 1828) Figs 224–226

*v 1828 *Strombus lineolatus* Wood: 13; pl. 4 (Strombus), fig. 11.

*v 1828 *Melania* (ex *Strombus*) *lineolatus* Wood: 42 (index).

. 1834 *Melania lineolata* Gray, *in* Griffith & Pidgeon: 598; pl. 13, fig. 4.

. 1840 *Hemisinus lineolatus* (Gray) Swainson: 341.

. 1847 *Hemisinus lineolatus* (Gray); Gray: 153.

. 1854 *Hemisinus lineolatus* (Wood); H. & A. Adams: 302.

. 1858 *Hemisinus lineolatus* (Wood); H. & A. Adams: pl. 32, figs 2, 2a, b.

. 1859 *Hemisinus lineolatus* (Gray); Chenu: 291, fig. 1995.

v. 1860 *Hemisinus lineolatus* (Gray); Reeve: pl. 1, figs 4a, b.

*v 1860 *Hemisinus buccinoides* Reeve: pl. 1, fig. 3.

. 1878 *Hemisinus lineolatus* (Gray); Brot: 373 (*pars*); pl. 38, figs 6, 6a–c.

. 1885 *Semisinus lineolatus* (Gray) Fischer: 701.
. 1902 *Hemisinus lineolatus* (Gray); von Ihering: 672.
? 1914 *Hemisinus lineolatus* (Gray); Vernhout: 36.
. 1939 *Hemisinus (Hemisinus) lineolatus* (Gray); Wenz: 718, fig. 2075.
. 1954 *Aylacostoma (Hemisinus) lineolata* (Gray) Morrison: 377.
? 1956 *Hemisinus lineolatus* (Gray); Pain: 103 (*pars*), figs 11a, b.

LECTOTYPE of *Strombus lineolatus* Wood (selected herein), the largest of four unlocalized Recent shells, Gray Colln, BMZD 1984206; the remaining shells are paralectotypes. The holotype of *Hemisinus buccinoides* Reeve (Recent, Jamaica; Cuming Colln) is BMZD 1984208.

OTHER MATERIAL STUDIED (All BMZD, Recent). Three shells, Venezuela (Cuming Colln); four shells (E. Chitty Colln), four shells (Mrs Longstaff Colln), 12 shells (Trechmann Colln), all Jamaica; several unlocalized shells, no history, including embryonic shell BMZD 1984207.

FURTHER RECORDS. All Recent. Distribution: Venezuela, Pernambuco (Reeve 1860); Brazil, Venezuela, the Guianas and Jamaica (Pain 1956: 103–105, table). Unknown fossil.

DIAGNOSIS. Almost smooth *Hemisinus*; spire angle 30°; spiral sculpture of faint grooving not covering all of shell; growth lines except on earliest whorls very weakly curved; whorls barely convex, waisted below suture; last whorl slightly swollen; earliest whorls smooth except for markedly opisthocline growth lines; colour patterning of brown spiral lines or dashes on offwhite to pale brown or grey background. Operculum as for genus. Parthenogenetic.

DESCRIPTION. The apex is present in several specimens including the lectotype, and is well preserved in one of the accompanying paratypes, as well as in shells from Jamaica and Venezuela (Chitty and Cuming Collns, respectively). It is absent in the holotype of *H. buccinoides*. The first whorl is virtually flush with the apex; the second is embraced by the succeeding whorl above the periphery but the suture drops away steeply so that more of the third whorl is visible, with the suture eventually lying below its periphery. The opisthocline growth lines are strong but no spiral sculpture is present. In these early whorls the shell is semi-transparent and three or four septa plugging the earlier-formed parts of the spire may be seen. The later shell surface is fairly smooth except for the growth lines and indications of weak grooving, mainly confined to the last whorl or so, and not persisting onto the neck region of the body whorl. The whorls are only weakly convex in profile, later ones being both more strongly convex and also waisted below the suture. In larger shells the outer lip is slightly flared; evidence of several previous apertures may be found on the last whorl, but no proper varices are formed. In both the lectotype and the holotype of *H. buccinoides* the callus high on the inner lip is swollen into a weak ridge, constricting the adapical extremity of the aperture. An embryonic shell (BMZD 1984207) extracted from an unlocalized specimen has five whorls and a height of 4.6 mm.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Lectotype of *H. lineolatus*	39.8	16.2	15.0	2.65	30°
Holotype of *H. buccinoides*	37.1 (eh = 40)	17.2	15.3	2.42	32°

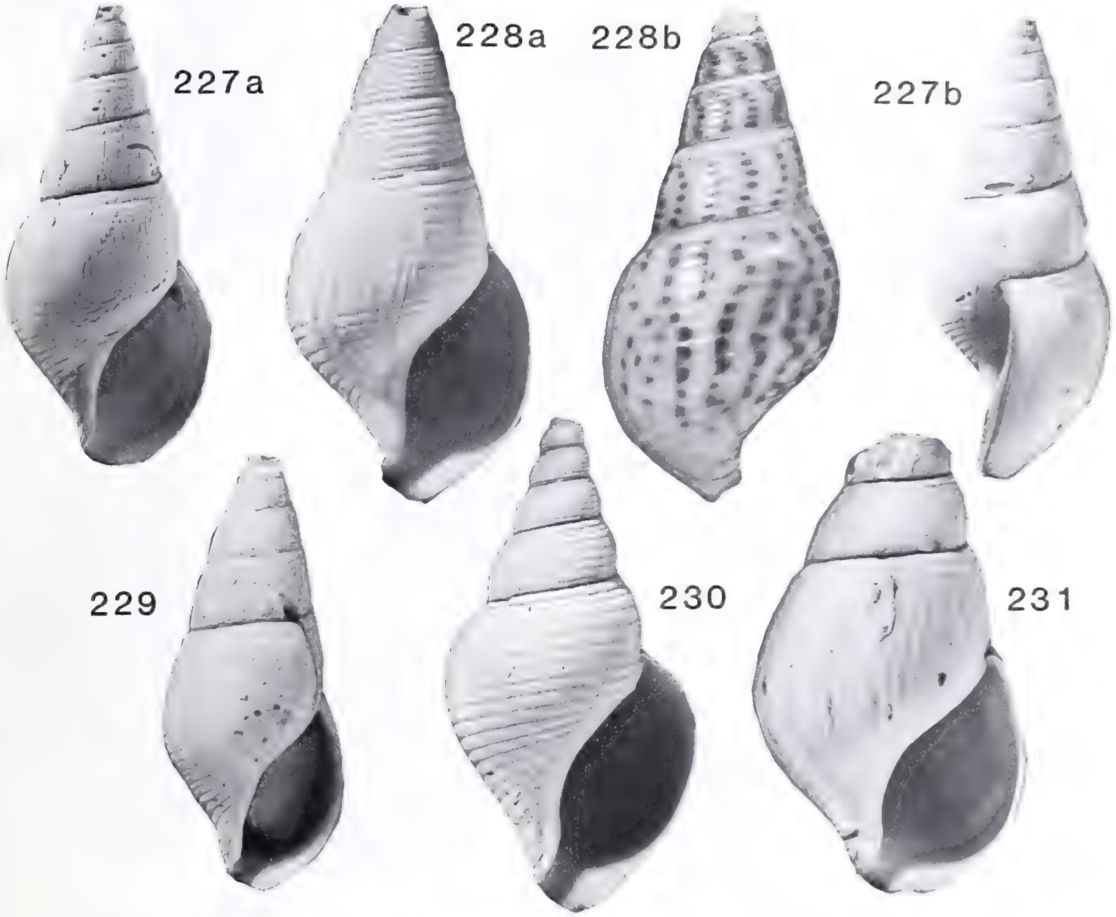
REMARKS. Wood's (1828) illustration is reduced but it is marked (a +), thus indicating a shell size of about 1½" (38 mm). Only the specimen selected here as lectotype is of about this size: the three paralectotypes are 24–28 mm high, and would thus have fallen into the 'one inch' bracket in the notation adopted by Wood.

This species is distinguished from the very similar *H. brasiliensis* by its lack of a properly developed pattern of spiral grooving. More importantly the earliest whorls – which correspond to the embryonic shell – of the two species may also be distinguished on a similar basis. *H. lineolatus* is smooth except for growth lines whilst *H. brasiliensis* is spirally ridged from the earliest stages. Both Brot (1878) and Pain (1956) include *H. punctatus* Reeve in the synonymy of *H. lineolatus*. The two appear similar in early illustrations (Wood 1828, Reeve 1860, Brot 1878) showing the orange-brown spiral colour patterning, the differences in sculpture not being apparent. *H. punctatus* is spirally striate: unfortunately its apical whorls are unknown. Pain remarked (1956: 104) that *H. lineolatus* was known from the Black River in Jamaica, but was otherwise unknown in the West Indies; he suggested that the Guiana occurrence might be an introduction by man from Jamaica. There is no evidence for this, nor for the opposite and equally plausible supposition that the species was introduced to Jamaica from South America. The distribution data is both suspect and anomolous. The fact that several BMZD samples give the locality as Jamaica suggests that the species does occur on that island. The similarities in shape, size and coloration between *H. lineolatus* and *H. brasiliensis* (Moricand), which occurs in Venezuela, brings into question the accuracy of some earlier reports: the habit of adding locality data to unlocalized specimens on the basis that they had been described from a particular locality was all too prevalent.

Hemisinus kochi (Bernardi, 1856) Figs 227–242

* 1856 *Melania kochi* Bernardi: 83; pl. 3, fig. 6.
v. 1860 *Hemisinus kochi* (Bernardi) Reeve: pl. 5, fig. 21a–d.
*v 1860 *Hemisinus punctatus* Reeve: pl. 1, figs 1a, b.
*v 1860 *Hemisinus pulcher* Reeve: pl. 4, figs 15a, b.
*v 1860 *Hemisinus zebra* Reeve: pl. 4, figs 15c, d.
*v 1860 *Hemisinus obesus* Reeve: pl. 4, figs 17a, b.
*v 1860 *Hemisinus globosus* Reeve: pl. 6, fig. 26.
. 1878 *Hemisinus lineolatus* (Gray); Brot: 374 (*pars*).
. 1878 *Hemisinus pulcher* Reeve; Brot: 387; pl. 40, figs 6a, b.
. 1878 *Hemisinus globosus* Reeve; Brot: 388; pl. 40, fig. 3
. 1878 *Hemisinus zebra* Reeve; Brot: 389; pl. 40, figs 11, 11a.
v. 1878 *Hemisinus obesus* Reeve; Brot: 389; pl. 40, fig. 7.
. 1902 *Hemisinus zebra* Reeve; von Ihering: 670, 680.
. 1902 *Hemisinus obesus* Reeve; von Ihering: 670.
. 1902 *Hemisinus pulcher* Reeve; von Ihering: 671, 680.
. 1902 *Hemisinus globosus* Reeve; von Ihering: 671, 680.
. 1902 *Hemisinus kochi* (Bernardi); von Ihering: 671.
v. 1938 *Semisinus sulcatus* (Conrad) de Greve: 99, text-fig. 23; pl. 4, figs 17–19, 21–25.
. 1969 *Aylacostoma sulcatus* (Conrad) Parodiz: 141 (*pars*), not pl. 14, figs 6, 7.

MATERIAL STUDIED. For convenience, due to the number of syntypic series examined, this is divided into (a) type



Figs 227–231 *Hemisinus kochi* (Bernardi). Recent, Brazil. **227**, BMZD 1984209/1; **lectotype** (selected herein) of *Hemisinus punctatus* Reeve, figured by Reeve (1860: pl. 1, figs 1, 1a); 'Pernambuco' = Recife, Brazil; Cuming Colln. a, front, × 2; b, side, × 2. **228**, BMZD 1984209/2; previously unfigured paralectotype of *H. punctatus*; same details as lectotype. a, front, × 2; b, side, × 2. **229**, BMZD 1984209/3; previously unfigured paralectotype of *H. punctatus*; same details as lectotype; front, × 2.5. **230**, BMZD 1984210; specimen figured by Reeve (1860: pl. 5, fig. 21) as *H. kochi* (Bernardi); Brazil; Cuming Colln; front, × 2. **231**, BMZD 49.1.5.36; **lectotype** (selected herein) of *Hemisinus obesus* Reeve, figured by Reeve (1860: pl. 4, fig. 17); Para, Brazil; front, × 2.

designations and (b) further material studied. Many of the figures given in Reeve (1860) are not the same size as the specimens and details of the colour patterning are often inaccurate. Some of the data given was also muddled. Specimens of *Melania* from Para, Brazil, were bought at Stevens' sale and registered in 1849 as BMZD 1849.1.5.28–40. Numbers 36–40 are the syntypes of *H. obesus* Reeve, which Reeve stated were in the Cuming Collection, bought by BM in 1866. Numbers 28–31 and 32–35 are *H. globosus* Reeve and *H. pulcher* Reeve, respectively. It seems possible that these specimens might also be syntypic material.

TYPE DESIGNATIONS. Lectotype (selected herein) of *Hemisinus punctatus* Reeve. Shell figured Reeve (1860: pl. 1, figs 1a, b) and two unfigured paralectotypes. Recent, 'Pernambuco' = Recife, Brazil; Cuming Colln, BMZD 1984209.

Lectotype (selected herein) of *Hemisinus obesus* Reeve, BMZD 49.1.5.36, shell figured Reeve (1860: pl. 4, fig. 17) and four paralectotypes, BMZD 49.1.5.37–40. Recent, Para, Brazil.

Lectotype (selected herein) of *Hemisinus pulcher* Reeve. Shell figured Reeve (1860: pl. 4, figs 15a, b) and two unfigured paralectotypes. Recent, Pernambuco; Cuming Colln, BMZD 1984211.

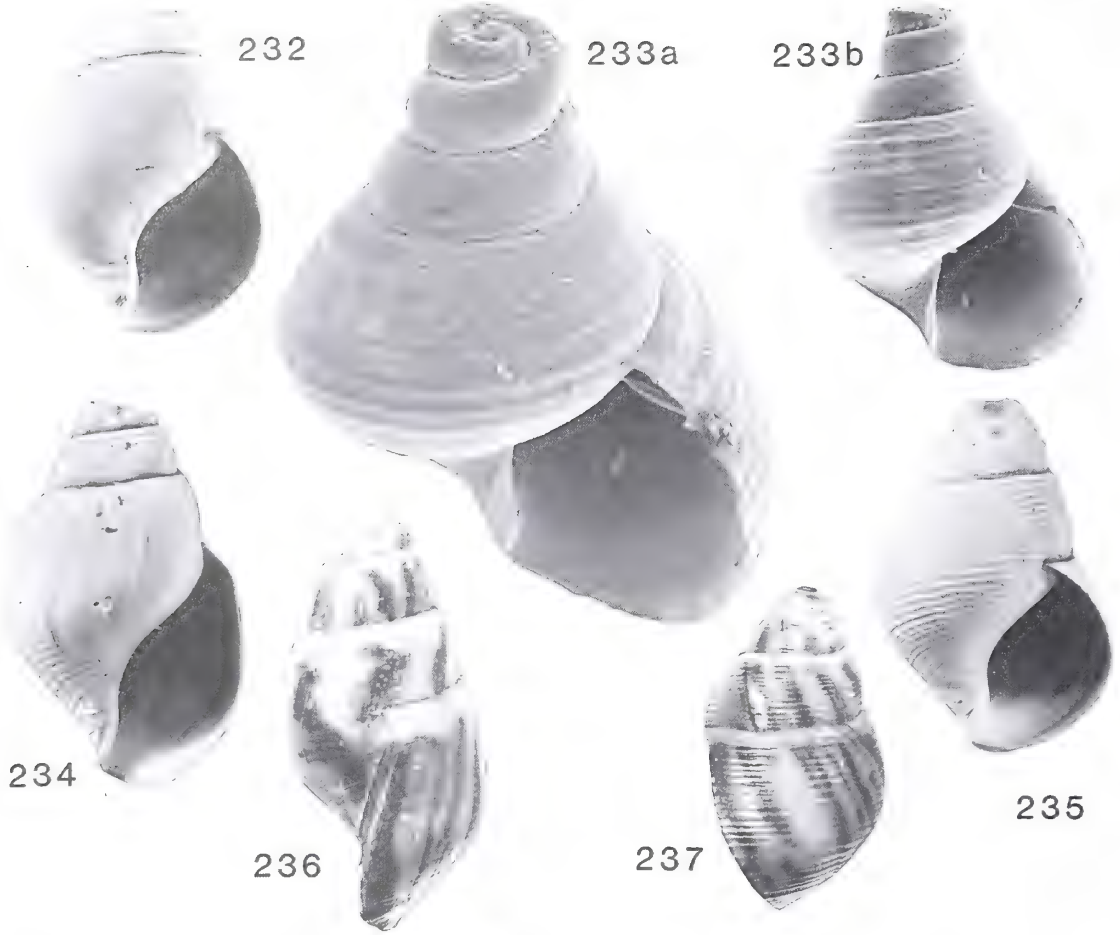
Lectotype (selected herein) of *Hemisinus zebra* Reeve. Shell figured Reeve (1860: pl. 4, figs 15c, d) and two unfigured paralectotypes. Recent, Pernambuco; Cuming Colln, BMZD 1984212.

Holotype of *Hemisinus globosus* Reeve. Recent, Pernambuco; Cuming Colln, BMZD 1984213.

FURTHER MATERIAL STUDIED. Recent: BMZD two shells figured as *Hemisinus kochi* Bernardi by Reeve (1860: pl. 5, fig. 21a, b and fig. 21c, d); Brazil, Cuming Colln, and one accompanying shell; BMZD 49.1.5.28–35, including (28–31) four shells and one embryonic shell labelled *H. globosus* Reeve; Para.

Fossil: All late Caenozoic, Iquitos, Peru, PIMUZ. Described and figured by de Greve (1938: pl. 4) as *Semisinus sulcatus* (Conrad): no. 312, figs 22, 23; no. 315, fig. 19; no. 317, figs 21, 24; no. 319, fig. 17; no. 321, fig. 18.

FURTHER RECORDS AND DISTRIBUTION. Recent, Brazil (Bernardi 1856). No author has given a more precise locality for specimens they identified as *H. kochi*. Reeve's (1860) nominal species were recorded from either Brazil or Pernambuco (= Recife) or Para: this locality data appears to be merely repeated by Brot (1878) and by von Ihering (1902). Fossil: Late Caenozoic, Iquitos (de Greve 1938), including an immature sinistral shell (1938: text-fig. 23).



Figs 232–237 *Hemisinus kochi* (Bernardi). Recent; 'Pernambuco' = Recife, Brazil; Cuming Colln. **232**, BMZD 1984213/1; holotype of *Hemisinus globosus* Reeve, figured by Reeve (1860: pl. 6, fig. 26a, b); front, × 2. **233**, embryonic shell obtained from inside holotype of *H. globosus*, BMZD 1984213/2. a, frontal oblique, × 36; b, front, × 20. **234**, BMZD 1984212/1; **lectotype** (selected herein) of *Hemisinus zebra* Reeve, figured by Reeve (1860: pl. 4, figs 15c, d); front, × 2. **235**, BMZD 1984212/2; one of the two previously unfigured paralectotypes of *H. zebra* Reeve; same details as lectotype; side, × 2. **236**, BMZD 1984211/1; **lectotype** (selected herein) of *Hemisinus pulcher* Reeve, figured by Reeve (1860: pl. 4, figs 15a, b); front, × 2. **237**, BMZD 1984211/2; one of two hitherto unfigured paralectotypes of *H. pulcher* Reeve; same details as lectotype; side, × 2.

DIAGNOSIS. Moderately stout, very variable *Hemisinus*; spire angle between 28° and 42°; subsutural grooving present; spiral sculpture of grooving varying from almost obsolete up to about seventeen grooves on spire whorls and double that number on body whorl; collabral sculpture lacking except for sigmoid growth lines of variable strength; whorl profile from slightly to moderately biconvex; shell colour white with brown axially arranged wavy lines of varying thickness, sometimes broken up into spots or dashes on interspaces between grooves; periostracum, brown. Soft parts, unknown; operculum typical of genus.

DESCRIPTION. The earliest part of the shell is almost always decollated and is unknown in any of the adult specimens. Embryonic shells, washed out of adults, have rather broad biconvex early whorls followed by up to two whorls in which the spiral grooving similar to that of the adult develops. Most of the features described in the above diagnosis vary considerably between different shells but remain fairly constant on any particular individual. The main exception to this is that the convexity of the last whorl is sometimes greater than that of preceding spire whorls.

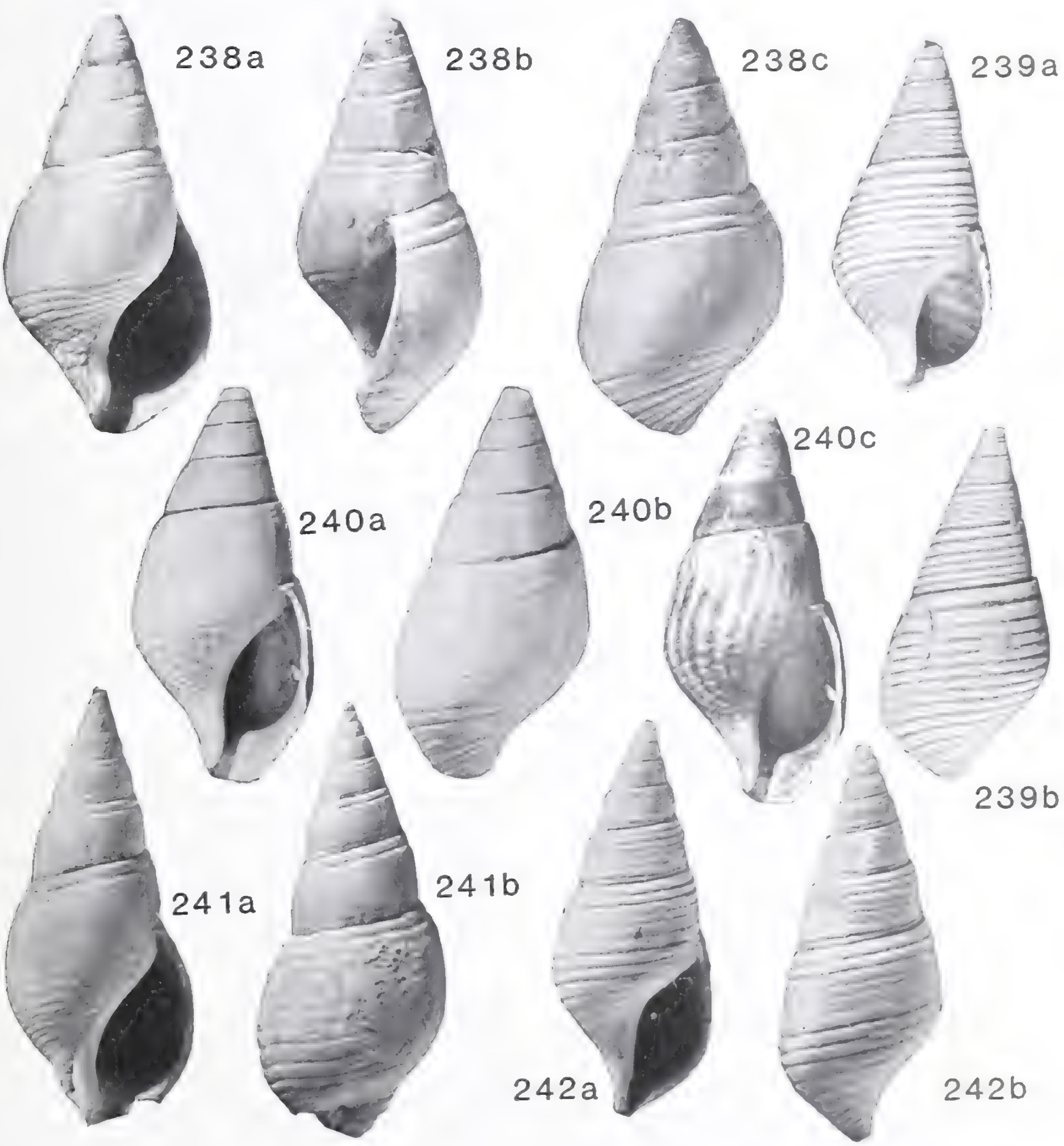
The colour pattern varies from one extreme of more or less collabral broad wavy bands, as exemplified by *H. zebra*, *H. pulcher* and *H. obesus*, to the other of collabrally arranged rows of dashes situated on the interspaces between the spiral grooves, with between seven and fifteen rows per whorl: such patterning is most developed on one of the paralectotypes of *H. punctatus*. Reeve's illustration of this species is composite, being made up of the strong colour patterning of this specimen superimposed on the outline of the lectotype.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Recent:					
Type illustration, *Melania kochi* Bernardi, 1856	30.6	15.4	14.6	1.99	38°
H. kochi (Bernardi), figd Reeve 1860: pl. 5, fig. 21	32.5	16.5	16.8	2.00	42°
Lectotype, *H. punctatus* Reeve	30.5	14.5	13.0	2.10	36°
Paralectotype, *H. punctatus* Reeve	25.7	12.7	12.8	2.15	36°
Paralectotype, *H. punctatus* Reeve	*22.9	9.6	11.9	–	28°
Lectotype, *H. obesus* Reeve	*30.3	18.2	15.5	–	40°
Lectotype, *H. pulcher* Reeve	*23.2	15.6	–	e1.5	52°
Lectotype, *H. zebra* Reeve	*25.0	15.3	–	e1.82	53°
Holotype, *H. globosus* Reeve	*20.8	14.7	–	e1.60	58°

* = decollated, or otherwise extensively damaged.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Fossil:					
PIMUZ 312, Iquitos	13.5	6.6	6.4	2.15	40°
PIMUZ 315, Iquitos	29.8	14.9	14.0	2.00	37°
PIMUZ 317, Iquitos	24.6	12.5	12.9	2.09	41°
PIMUZ 319, Iquitos	13.7	5.9	–	2.32	33°
PIMUZ 321, Iquitos	12.0	5.8	11.3	2.07	37°

REMARKS. Both Brot (1878) and von Ihering (1902) largely repeated Reeve, thus contributing relatively little new information. For instance, Brot's figure of *H. obesus* Reeve is a copy of the original illustration. The bulk of Reeve's material was said to be from Pernambuco (Recife) and shows strong links between the various nominal species that he described. Bernardi's type material of *H. kochi* has not been studied but the specimens figured in Reeve (1860) and Brot (1878) agree well with his original illustration (1856). Reeve's shells of *H. kochi* are also very close to the type series of his *H. punctatus*. Individual specimens in this series, in which the apical angle varies between 28° and 36°, may be linked with individual fossils from Iquitos (PIMUZ) originally identified by de Greve (1938) as *Semisinus sulcatus* Conrad, and subsequently quoted in the synonymy of this species given by Parodiz (1969). These Iquitos fossils clearly belong here rather than



Figs 238–242 *Hemisinus kochi* (Bernardi). Pebasian; Iquitos, Peru; specimens previously identified by de Greve (1938) as *Semisinus sulcatus* (Conrad). **238**, PIMUZ 317; shell figured by de Greve (1938: pl. 4, figs 21, 24). a, b, c, front, side, rear, all × 2.5. **239**, PIMUZ 321; shell figured by de Greve (1938: pl. 4, fig. 18). a, b, front, rear, × 4. **240**, PIMUZ 312; shell figured by de Greve (1938: pl. 4, figs 22, 23). a, b, c, front, rear, and front to show colour patterning, all × 4. **241**, PIMUZ 315; shell figured by de Greve (1938: pl. 4, fig. 19). a, b, front, rear, × 2. **242**, PIMUZ 319; shell figured by de Greve (1938: pl. 4, fig. 17). a, b, front, rear, × 4.

allied to *H. brasiliensis* (Moricand), (below), the senior synonym of *H. sulcatus* Conrad. *H. brasiliensis* exhibits far less variation than *H. kochi*. It is more acicular and its spiral grooving is much more regular in both numbers and intensity.

No specimens of the small (h = 20 mm) but superficially rather similar *Hemisinus schneideri* Brot (1878: 386; pl. 40, figs 2, 2a), described from the Rio Marañon, have been seen. Von Ihering (1902: 670) compared it with *Hemisinus [Melania] osculati* (Villa, 1857), which also occurs in the Upper Amazon and unspecified areas of Peru, Ecuador and Colombia (Brot 1878: 379, von Ihering 1902: 669). BMZD specimens identified as *Hemisinus aspersus* Reeve (1860), a species regarded by both these authors as one of the junior synonyms of *H. osculati* (Villa), lacks the apertural features of *Hemisinus*. The type series of *H. aspersus* cannot be found in BMZD.

Hemisinus brasiliensis (Moricand, 1838) Figs 243–247

*	1838	*Melanopsis brasiliensis* S. Moricand: 144; pl. 3, figs 12, 13.
.	1847	*Melania brasiliensis* (S. Moricand) Philippi: 169; pl. 4, fig. 1.
*v	1859	*Melania venezuelensis* (Dunker MS) Reeve: pl. 13, fig. 81.
v.	1860	*Hemisinus brasiliensis* (S. Moricand) Reeve: pl. 1, fig. 5.
*v	1860	*Hemisinus tenellus* Reeve: pl. 2, fig. 6.
.	1860	*Melanopsis brasiliensis* S. Moricand; J. Moricand: 301; pl. 12, fig. 7.
*v	1871*b*	*Hemisinus sulcatus* Conrad: 194; pl. 10, fig. 2.
.	1878	*Hemisinus venezuelensis* (Dunker) Brot: 391; pl. 40, fig. 10; pl. 41, figs 9, 9a.
.	1878	*Hemisinus brasiliensis* (S. Moricand); Brot: 392 (*pars*); pl. 40, figs 12, 12a–c.
.	1914	*Hemisinus brasiliensis* (S. Moricand); Pilsbry *in* Baker: 657.
.	1969	*Aylacostoma sulcatus* (Conrad) Parodiz: 141 (*pars*; not pl. 14, figs 6, 7).

MATERIAL STUDIED. NYSM 9226, the holotype of *H. sulcatus* Conrad, Pichana. The lectotype, selected herein, of *Melania venezuelensis*, the original of Reeve's (1859) pl. 13, fig. 81, and an unfigured paralectotype; Porto Cabello, Venezuela (BMZD 1984215, Cuming Colln). The lectotype, selected herein, of *Hemisinus tenellus*, the original of Reeve's (1860) pl. 2, fig. 6, and two unfigured paralectotypes; Pernambuco (BMZD 1984216, Cuming Colln). The shell figured by Reeve (1860: pl. 1, fig. 5) as *H. brasiliensis* (S. Moricand); Pernambuco (BMZD 1984214, Cuming Colln).

DISTRIBUTION. Recent: Villa de Barra, Bahia Province, Brazil (S. Moricand). Recife (Pernambuco), Brazil (Reeve). Venezuela (Reeve). Alcobaca, left bank, lower Tocantins River, Para Province, Brazil (Pilsbry *in* Baker).

Fossil: Late Caenozoic; Pichana (Conrad), Iquitos (de Greve).

DIAGNOSIS. Comparatively acicular *Hemisinus* with spire angle of *c*. 30°; whorls weakly biconvex in outline; spiral sculpture of six to eight narrow grooves on spire whorls with double the number on the body whorl and with strongest groove immediately below suture; collabral sculpture absent except for growth lines.

DESCRIPTION. There are 8 – 10 barely convex whorls. The aperture is about two-fifths shell height, the apical angle is between 28° and 33° and the height to breadth ratio about 2.5:1. The apices of all the available specimens are damaged. Only one shell (Fig. 245), the hitherto unfigured specimen found with that figured by Reeve (1859) as *M. venezuelensis*, shows details of the early stages. Its first whorl is badly damaged and the second, which is strongly convex and twice as broad as high, is worn. On it, two spiral bands appear: these are added to later at the lower suture so that by the fifth whorl there are six or seven and the appearance becomes typical of the adult. The earlier whorls, however, differ from later ones in several respects. They are much more inflated, with a ramp above, and a semi-incised suture below, separated by a comparatively straight-sided median portion. The three 'facets' of the whorl side are separated by well-rounded spiral cords. These convex cords are separated by relatively strong grooves. In later whorls, the cords broaden and become flat whereas the intervening grooves barely increase in strength. The spiral bands are of variable width and any variation appears to be random. In all specimens a subsutural band or collar is formed. Growth lines are the only collabral sculptural element. They are not strong but are clearly visible on all specimens. The aperture is smooth within. Light parietal callus is present only in the holotype of *H. sulcatus* Conrad: in all other specimens light callus is confined to the columella itself.

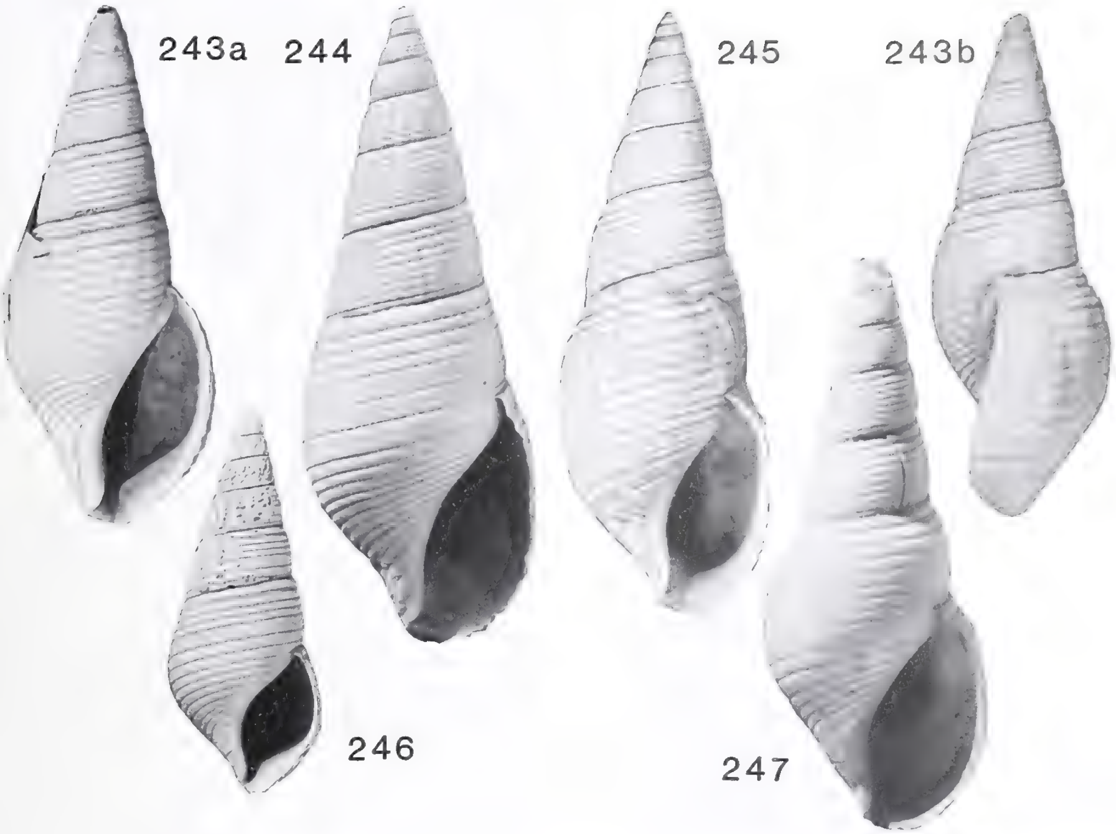
Colour patterning consists of about four elongate strong brown dashes arranged as more or less collabral rows on each spire whorl, with about eight to ten rows per whorl. There is a noticeable narrow light band just below the suture. There is a background coloration of a few alternate pale brown and light bands, which are visible through the thin periostracum and also on the inside of the outer lip.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
H. brasiliensis (Moricand), figd Reeve (1860: pl. 1, fig. 5).	33.8	12.4	14.2	2.64	28°
The accompanying shell	31.8	11.8	12.2	2.70	28°
H. tenellus Reeve. Lectotype (Reeve 1860: pl. 2, fig. 6).	25.2	10.1	11.8	2.5^+	29°
M. venezuelensis Reeve (*ex* Dunker MS). Lectotype (Reeve 1859: pl. 13, fig. 81).	19.9	8.0	7.8	2.49	30°
H. sulcatus Conrad. Holotype (excluding varix).	27.2	11.2	12.6	2.43	33°–30°

REMARKS. There seem to be no conchological reasons for keeping separate any of the species here included in the synonymy of *H. brasiliensis* (Moricand). The lectotype of *H. tenellus* Reeve has a more convex last whorl than other living shells – a feature shared with the holotype of *H. sulcatus* Conrad, and slightly reminiscent of the latter's varix. The paralectotypes of *H. tenellus* are fairly small and could easily be confused with the type series of *H. venezuelensis* (Reeve).

H. brasiliensis (Moricand) is very similar to the type species, *H. lineolatus* (Woods). The latter may be distinguished by its lack of spiral grooving. Illustrations showing its spiral colour patterning, can, however, give the false impression that it is grooved.

The holotype of *H. sulcatus* Conrad is here referred to *H. brasiliensis*, but all other specimens identified as *H. sulcatus* by subsequent authors are placed elsewhere. Those shells from Iquitos studied by de Greve (1938) are now identified as *H. punctatus* Reeve. Specimens from Três Unidos figured by Parodiz (1969) as *Aylacostoma sulcatus* are referred to *Verena*



Figs 243–247 *Hemisinus brasiliensis* (S. Moricand). **243**, NYSM 9226; holotype of *Hemisinus sulcatus* Conrad, figured by Conrad (1871: pl. 10, fig. 2); Pebasian; Pichana, Peru. a, b, front, side, × 2.5. **244**, BMZD 1984214/1; shell figured by Reeve (1860: pl. 1, fig. 5) as *H. brasiliensis*; Recent; 'Pernambuco' = Recife, Brazil; Cuming Colln; front, × 2.5. **245**, BMZD 1984214/2; previously unfigured shell from same sample as Fig. 244; front, × 2.5. **246**, BMZD 1984215; **lectotype** (selected herein) of *Melania venezuelensis* Reeve, figured by Reeve (1859: pl. 13, fig. 81); Recent; Porto Cabello, Venezuela; Cuming Colln; front, ×2.5. **247**, BMZD 1984216; **lectotype** (selected herein) of *Hemisinus tenellus* Reeve, figured by Reeve (1860: pl. 2, fig. 6); 'Pernambuco' = Recife, Brazil; Cuming Colln; front, × 2.5.

browni Etheridge. The material from Loc. 42, Mangán Formation in the Cuenca Basin described but not figured in Bristow & Parodiz (1982: 47) as *Aylacostoma sulcatus* is here reidentified as *Hemisinus* sp. (GG21225/1–6, p. 246). *Aylacostoma* sp. (GG19866/1–3, p. 261) also occurs at this locality.

Hemisinus (s.l.) *corrosensis* Pilsbry & Olsson, 1935

Fig. 248

v* 1935 *Hemisinus (Basistoma) corrosensis* Pilsbry & Olsson: 12; pl. 2, figs 8, 9.

v 1969 *Doryssa corrosensis* (Pilsbry & Olsson) Parodiz: 136.

HOLOTYPE. ANSP 13092, originally figured by Pilsbry & Olsson (1935: pl. 2, fig. 8). Los Corros Formation, Tertiary; Rio Succio, a branch of Rio Llano, Magdalena Valley, Colombia (Olsson & La Tour Collection). An unknown number of paratypes (not seen) are stated to be in Olsson's collection (Pilsbry & Olsson: 12), and include the specimen figured originally as pl. 2, fig. 9. Other details as above. No further material.

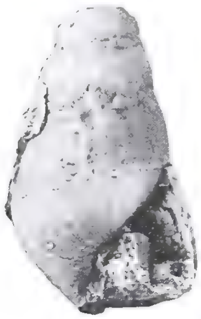
DIAGNOSIS. *Hemisinus* with spire angle of 30°; early whorls smooth; spiral sculpture of 5 – 6 grooves on later spire whorls and 10 – 12 on final whorl; collabral sculpture lacking, growth lines weakly reverse sigmoid; whorls very weakly convex; sutures simple.

DESCRIPTION. The holotype is now broken into two parts. The spire is acute. The whorls are weakly convex, with the periphery just above the suture. Sculpture other than growth lines cannot be seen on the early whorls but there are five spiral grooves of unequal width on the penultimate whorl and about double this number of the final whorl as the grooving continues onto the neck. Collabral sculpture is absent except for the growth lines. Those on the smaller spire fragment do not reveal whether the basal apertural notch typical of Hemisininae was present. The aperture is pointed above, not rounded.

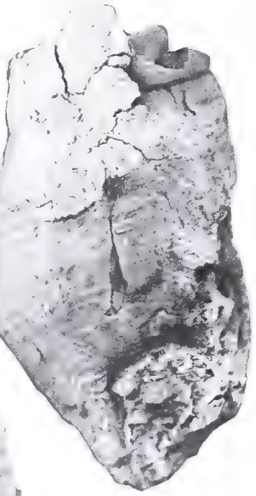
DIMENSIONS (from Pilsbry & Olsson). ANSP 13092 (holotype): h, 29 mm; br, 11 mm.

REMARKS. Pilsbry & Olsson referred to 'The Type' and to 'Paratypes'. The 'Type' is therefore taken to be the holotype, whose published dimensions fit those of the now broken ANSP 13092 (br = 10.7 mm). Pilsbry & Olsson's illustration (1935: pl. 2, fig. 8) is extensively retouched, and greatly enhances the very weak spiral grooving. They defined (1935: 11) *Basistoma* as being spirally grooved or corded and presumably assigned *H. corrosensis* to it for that reason. The aperture is, as far as can be judged from the damaged holotype, low in relation to the height of the spire, as in *Basistoma*. As growth lines can be seen on the early whorls of the holotype, it is clear that spiral grooving is truly absent, rather than missing on account of poor preservation. This lack of early spiral sculpture is more suggestive of *Hemisinus* and *Sheppardiconcha* than of *Basistoma*. The aperture in *Sheppardiconcha* tends to be more rounded above. This species is therefore provisionally assigned to *Hemisinus*. It does not appear to belong to *Doryssa* similar to *D. atra*, as suggested by Parodiz (1969), who was basing his decision on the original description and illustrations of *H. corrosensis*, not on new material.

The allegedly Eocene specimens identified by Boss & Parodiz (1977: 118, figs 10, 11) as *Doryssa corrosensis* (Pilsbry & Olsson) from Isla Navarra, Rio Huallaga, San Martin, Peru, appear to be misidentified. The illustrations are of internal moulds on which traces of spiral sculpture can be clearly seen.



248a



248b

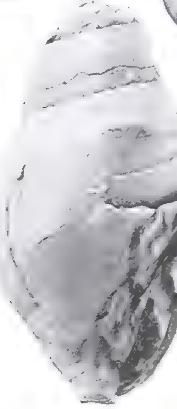


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Fig. 248 *Hemisinus corrosensis* Pilsbry & Olsson. ANSP 13092; damaged holotype, figured by Pilsbry & Olsson (1935: pl. 2, fig. 8). Palaeogene, Los Corros Formation; Rio Succio, Middle Magdalena Valley, Colombia; E. La Tour Colln. a, b, top and bottom portions, × 3.

Fig. 249 *Hemisinus* sp. GG21225/1; Miocene, Mangán Formation; Loc. CRB 42, Cuenca Basin, Ecuador; Bristow Colln. × 2.

Hemisinus sp. Fig. 249

v 1982 *Aylacostoma sulcatus* (Conrad); Parodiz *in* Bristow & Parodiz: 47 (*pars*).

MATERIAL STUDIED. GG22125/1–6; Loc. CRB 42, Mangán Formation, ? late Miocene, Cuenca Basin, Ecuador. No further records.

DIMENSIONS. GG22125/1: h, 20.7 mm; eh, 26.5 mm; br, 10.6 mm.

DESCRIPTION. The specimens studied are all damaged. The shell is relatively acicular with an apical angle of between 35°–40°. No spiral ribbing is present. Collabral sculpture is absent except for the growth lines which are only moderately sinuate. The whorl profile is only weakly biconvex with the periphery at the lower suture. The apertural features cannot be made out properly. Columellar callus is present but the parietal region is never clearly enough exposed to show whether callus is developed. Growth lines near the columella show that the typical *Hemisinus* basal notch is present.

REMARKS. Parodiz quoted no registration numbers so it is not clear whether his work was based on specimens in Carnegie Museum as well as those in BMPD. He commented on the variability of the material. Here, the sample from CRB 42 is divided into the present species and *Aylacostoma* sp. (GG19866/1–3), p. 261. Although many characters may be clearly seen, the species is not named on the present material because it is comparatively poorly preserved. It can be distinguished from *H. braziliensis* (Moricand) by its lack of spiral ribbing. *H. kochi* (Bernardi) sometimes almost lacks spiral ribbing but its growth lines are much more sinuate. *H. lineolatus* (Wood) is almost smooth but always has some subsutural grooving. Western South American species only provisionally accepted herein as possible *Hemisinus*, such as *H. aspersus* Reeve (1860), *H. osculati* (Villa, 1857) and *H. schneideri* Brot (1878) all apparently have a much less developed basal notch.

Genus ***LONGIVERENA*** Pilsbry & Olsson, 1935

TYPE SPECIES. *Aylacostoma tuberculata* Spix (*in* Spix & Wagner 1827: pl. 8, fig. 4), by subsequent designation of Wenz (1939: 719); Recent, Brazil.

DIAGNOSIS. Like *Aylacostoma* but sculptured with strong spiral tuberculate ribs and collabral folds; operculum as in *Aylacostoma*; ovoviviparous ? parthenogenetic; embryonic shell with spiral ribbing.

OTHER SPECIES ASSIGNED. Fossil: *Hemisinus (Longiverena) eucosmius* Pilsbry & Olsson, 1935, Tertiary (? Neogene) of Colombia, Miocene of Ecuador, Late Caenozoic, Pebasian of Peru; *Hemisinus (Longiverena) mugrosanus* Pilsbry & Olsson, 1935, Tertiary (? Neogene) of Colombia; *Longiverena colombiana* sp. nov. (p. 249), Late Caenozoic, La Tagua. Recent: None.

DISTRIBUTION. ? Neogene only: Colombia, Ecuador, Peru. Recent: eastern Brazil.

REMARKS. Pilsbry & Olsson (1935) erected *Longiverena* as a 'section' of *Hemisinus* for elongate shells with rounded whorls sculptured with spiral cords or grooves and axial folds or ribs. This was to accommodate several mid-Tertiary species they were describing from the Magdalena Valley. They listed the various 'sections' of *Hemisinus* that they recognized along with one species of each which happened to be living and, in the case of the established taxa, was also the type species; these were *Hemisinus lineolatus* Gray, *Basistoma edwardsi* (Lea) and *Verena crenocarina* Spix (*sic*). The species they mentioned for *Longiverena* was *tuberculata* Spix. However, they gave no type designation, though it seems clear that *tuberculata* would have been their choice, and Wenz (1939) designated this as type species. Morrison (1952, not seen;

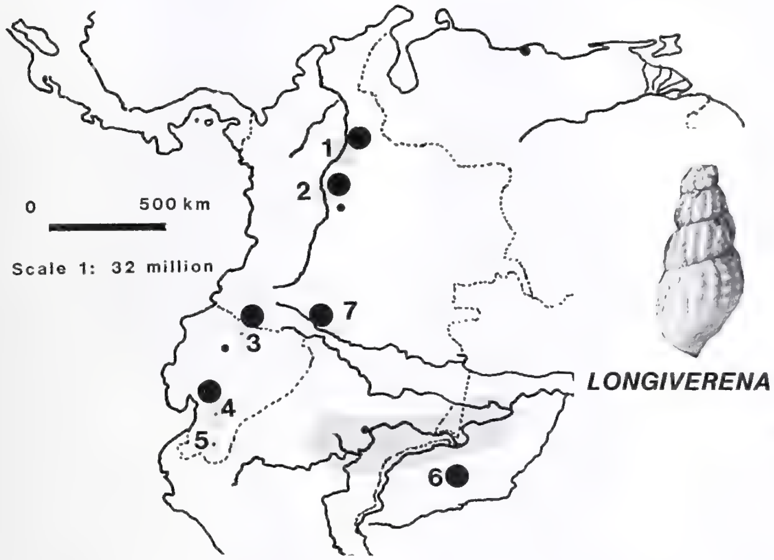


Fig. 250 Neogene distribution of *Longiverena*. Key as for Fig. 6 (p. 177). Inset: *L. eucosmia* (Pilsbry & Olsson), × 2; Mugrosa formation; Magdalena Valley, Colombia.

1954: 377) independently made the same choice; his 1952 paper was an abstract of a meeting report and is possibly not valid.

Wenz (1939: 719) gave the distribution of the genus as being Oligocene, ?Europe; Oligocene, Colombia; Recent, South America and West Indies. I am unaware of any species from outside South America.

Aylacostoma glabrum Spix and *Longiverena tuberculata* (Spix) appear to be very similar in many important respects except that *L. tuberculata* is strongly sculptured whilst *A. glabrum* is almost smooth. In the future, increased understanding of the South American fauna may lead to this distinction being regarded as not of generic significance. This would, however, raise the problem of the generic assignment of the fossil species, with the exception of *L. colombiana* sp. nov., here placed in *Longiverena*, as they would be most unlikely to fit comfortably in *Aylacostoma* in any future reclassification.

Longiverena tuberculata (Spix, *in* Spix & Wagner 1827)

Figs 251–255

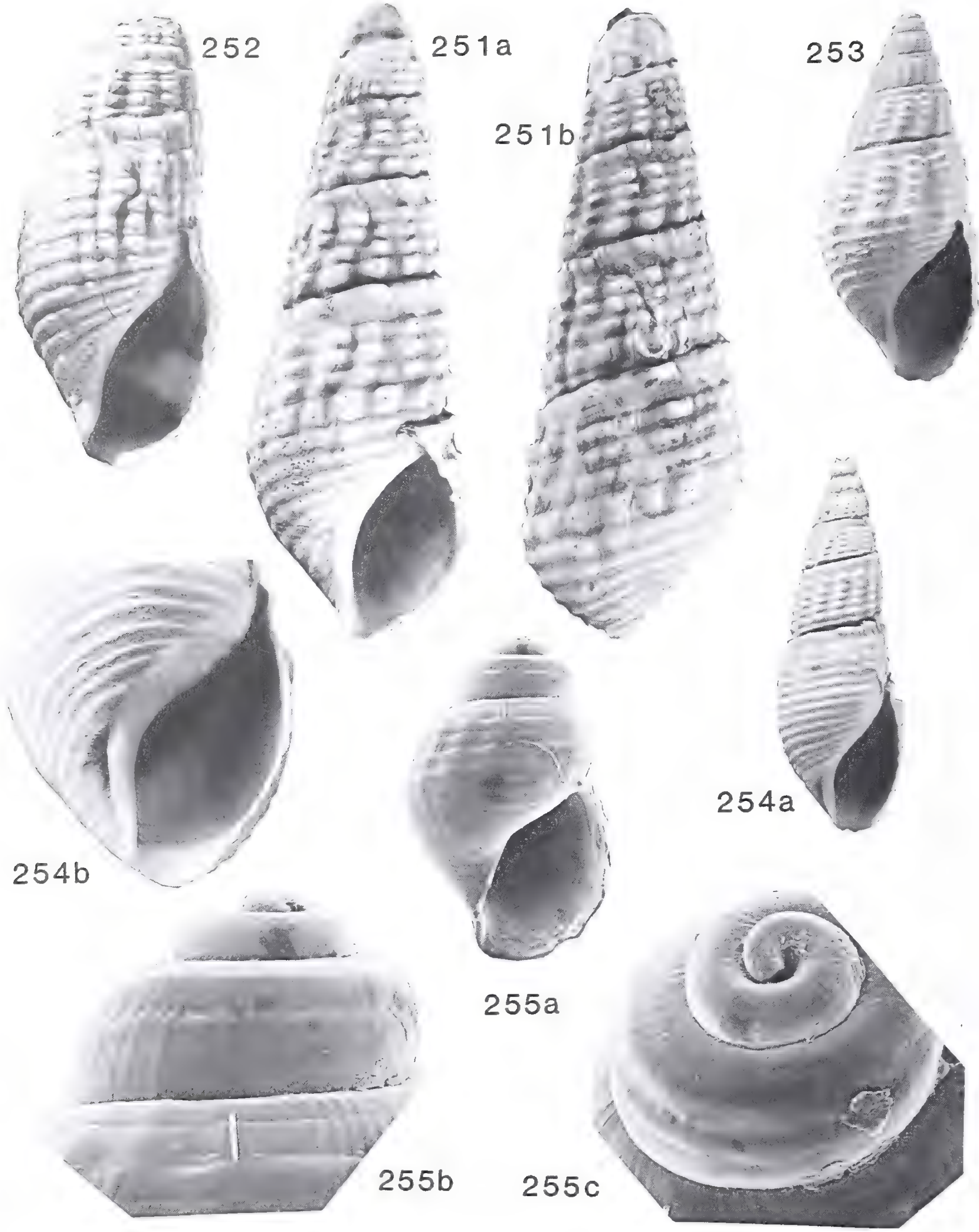
*v 1827 *Aylacostoma tuberculata* Spix, *in* Spix & Wagner: pl. 8, fig. 4.
v. 1827 *Melania tuberculata* Wagner, *in* Spix & Wagner: 15.
*v. 1860 *Hemisinus olivaceus* Reeve (*ex* Behn MS): pl. 3, fig. 12a, b.
. 1878 *Hemisinus tuberculatus* (Wagner) Brot: 397; pl. 41, figs 10, 10a–d.
. 1902 *Hemisinus tuberculatus* (Wagner); von Ihering: 667
. 1935 *Hemisinus (Longiverena) tuberculatus* (Spix); Pilsbry & Olsson: 11.
. 1939 *Hemisinus (Longiverena) tuberculatus* (Wagner); Wenz: 719, fig. 2078.
. 1954 *Aylacostoma (Longiverena) tuberculata* Spix; Morrison: 377.
. 1983*a* *Aylacostoma tuberculata* Spix = *Melania tuberculata* Wagner; Fechter: 222.

LECTOTYPE (selected herein) of *A. tuberculata* Spix, the specimen almost certainly figured by Spix 1827; the nine accompanying shells are paralectotypes. Recent, Mandiocca, Prov. St Sebastian, southern Brazil (Wagner, 1827). Staats. Zool. Mus. München (Spix Colln). The lectotype (selected herein) of *Hemisinus olivaceus* Reeve is the specimen figured by Reeve (1860); the two accompanying shells are paralectotypes. Recent, Pernambuco; Cuming Colln, BMZD 1984217.

OTHER MATERIAL. Fifteen adult and two embryonic shells; Recent, Brazil, BMZD 69.6.2.21, examined. Also recorded from the Recent of Rio de Janeiro by Ihering (1902). Distribution Recent only, Brazil.

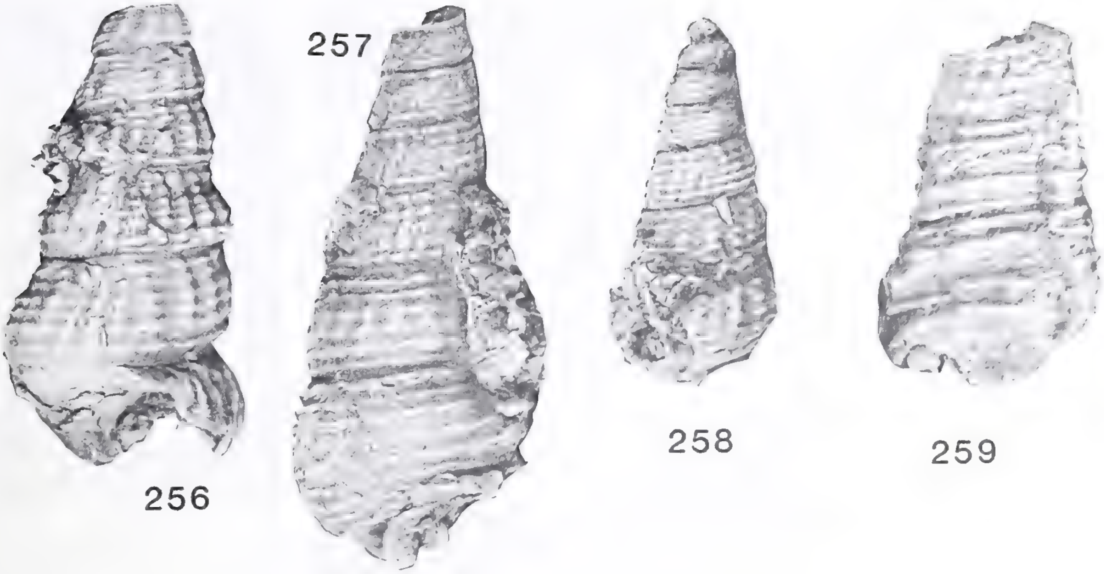
DIAGNOSIS. *Longiverena* with spire angle of about 20°; early whorls convex-sided, expanding moderately rapidly; shoulder of varying strength developed on later whorls.

DESCRIPTION. Most specimens are decollated. If complete, they would be up to 50 mm in height, with the aperture about one third shell height, and comprise ten whorls. The incremental angle is moderately obtuse for the early whorls but soon reduces to about 20° for the later whorls. Two embryonic shells extracted from adults in sample BMZD 69.6.2.21 have reached the stage where the adult type of sculpture is developed. Examination of these embryonic shells and those of young snails with a separate existence from the same sample has failed to detect any differences, such as change in sculpture, which might mark the transition from life in the oviduct to life outside it. The embryonic shell has about four whorls. The first two are wide, convex-sided, and rather sunken; the third has two spiral ribs increasing in number to six. The third and fourth whorls are strongly convex. On succeeding whorls a subsutural constriction is present, which sometimes develops into a ramp of varying strength. The whorl side below the shoulder is virtually straight-sided except for some constriction at the lower suture, with the periphery lying just above. Spiral sculpture consists of 5–6 ribs on the spire whorls and 10–14 on the final whorl. Traces of secondary ribbing occur on some specimens including the lectotypes of both *L. tuberculata* and *L. olivacea*. The ribs are

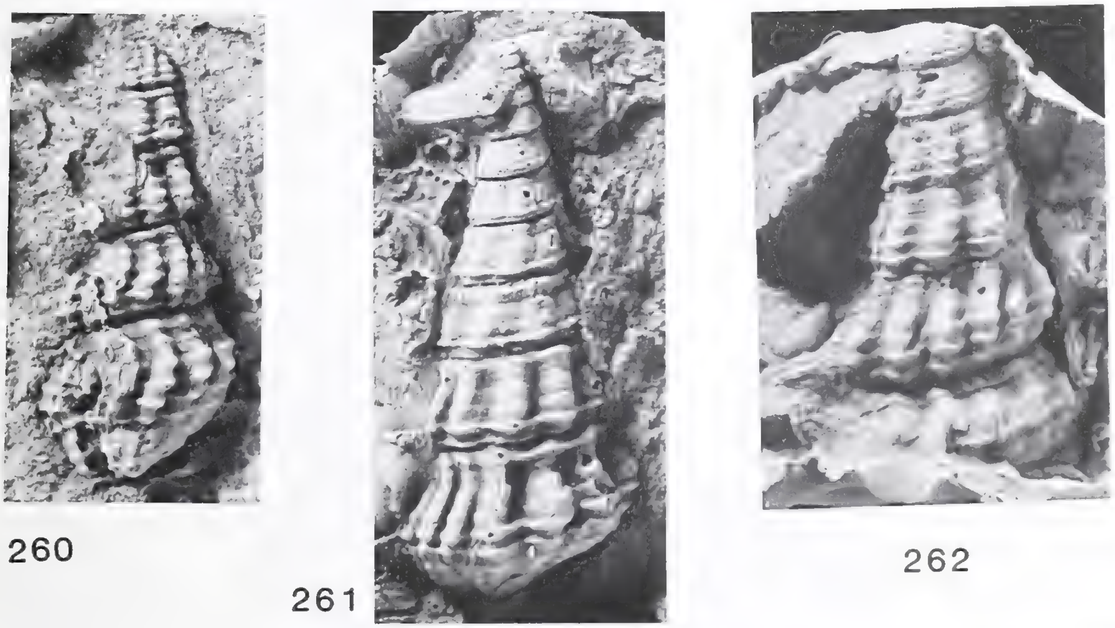


Figs 251–255 *Longiverena tuberculata* (Spix). Recent, Brazil. **251**, **lectotype** (selected herein) of *Aylacostoma tuberculata* Spix, figured by Spix (1827: pl. 8, fig. 4). Mandiocca, St Sebastian Province, southern Brazil; Spix Colln, Staats. Zool. Mus. München. a, b, front, rear, × 2.5. **252**, BMZD 1984217; **lectotype** (selected herein) of *Hemisinus olivaceus* Reeve, figured by Reeve (1860: pl. 3, figs 12a, b). Brazil. Front, × 3. **253–255**, all from same sample BMZD 69.6.2.21 of *L. tuberculata*, Brazil; Mrs Burton Colln. **253**, front, × 3. **254**, a, front, × 1.5; b, oblique view of neck of body whorl and aperture, × 3. **255**, embryonic shell extracted from adult in same sample; a, front, × 20; b, apex, × 50; c, oblique view of apex, × 50.

of varying width, most are well rounded but the two most adapical rows tend to develop pointed tubercles where they cross the underlying collabral folds. In the troughs between these folds the spiral ribbing tends to be weak. The number of collabral folds decreases from as many as twenty on early whorls to 10–15 on later whorls. The growth lines are weakly opisthocyrt on spire whorls and, at the aperture, form a reverse sigmoid labrum. The aperture is constricted above into a weak canal, and is notched below. The inner lip is callused, but the parietal region is only weakly so in smaller shells.



Figs 256–259 *Longiverena colombiana* sp. nov. Late Caenozoic; La Tagua, Colombia; Eden Colln. **256**, GG19943; **holotype**, Loc. 33/480–560; front, ×2.5. **257–259**, paratypes. **257**, GG19944; Loc. 33/480–560, × 2.5. **258**, GG19945; Loc. 33/480–560, × 2.5. **259**, GG19941; Loc. 54, × 5.



Figs 260–262 *Longiverena colombiana* sp. nov. Paratypes, latex casts of external moulds. Late Caenozoic; Loc. 44, La Tagua, Colombia; Eden Colln. **260**, GG21573; × 2. **261**, GG21572; × 4. **262**, GG 21574; × 4.

Dimensions. In mm.	h	br	hap	hbw	h/br	sa
Lectotype of *Aylacostoma tuberculata*, Staats. Zool. Mus. Munchen	*38.0	13.2	12.4	22.0	e3.1	20°
Lectotype of *Hemisinus olivaceus*, BMZD	*23.6	10.3	12.0	18.0	–	20°
BMZD 69.6.2.21	36.7	13.4	13.1	20.6	2.74	21°
BMZD 69.6.2.21	18.5	8.1	7.5	12.2	2.28	32°

* = decollated

Remarks. Spix' collection contained ten shells of this species. The shell here selected as lectotype is the only one which could be his figured specimen. Comparisons between this species and the fossil species assigned to *Longiverena* are given under the latter.

Longiverena colombiana sp. nov. Figs 256–262

Holotype. BMPD GG19943; Late Caenozoic; Loc. 33/480–560 cm, La Tagua (Eden Colln). The following are paratypes: GG19944–7, GG19991/1–5, information as above; GG19992 3, Loc. 33/570–670 cm; GG19941–2, Loc. 54; GG21572–4, Loc. 44; all La Tagua (Eden Colln).

Name. 'Colombian'.

Diagnosis. Medium-sized *Longiverena* with sculpture of about six evenly-spaced angular spiral ribs separated by wide interspaces and on later whorls crossing up to 20 strongly curved collabral folds per whorl; whorls comparatively broad; sutures incised; early whorls straight-sided, later whorls convex with periphery low down.

DESCRIPTION. All the apices and apertures are broken. In addition, most of the shells are partly crushed and the shell surface is seldom particularly well preserved. It is estimated that the height of the largest specimens would have been between 30 and 35 mm and the spire angle about 25°. The rate and sequence of development of the sculpture appears to be inconstant: some early whorls are smooth except for a prominent spiral rib above the incised lower suture, sometimes accompanied by a rather less prominent rib forming a subsutural collar. The rest of the spiral sculpture develops from grooves which rapidly broaden to form wide interspaces between narrow sharp ribs. The collabral folds are strongly opisthocyrt and vary in strength from specimen to specimen but are of reasonably constant strength in any one individual. Their spacing is also fairly constant so their number increases with whorl diameter, up to a maximum of 20 by the last whorl. The folds die away towards the lower suture and seldom affect the lowest spiral rib. GG19942, a crushed juvenile specimen, shows fine reticulate sculpture between the spiral ribs of early whorls. In adult specimens a callus pad is developed on the parietal region of the inner lip; other apertural features are not shown on the available material.

DIMENSIONS. Holotype, GG19943: h, 24.7 mm, e34 mm; br 12.9 mm; sa 25°.

REMARKS. This species may be distinguished from *L. tuberculata* (Spix) by its relatively broader whorls which never bear a shoulder, but the sculpture of the two species is closely similar. In *L. colombiana* there is no wide gap between the two most adapical ribs as there is in *L. tuberculata*. In addition, its opisthocyrt growth lines and collabral ribs are more evenly curved than those of *L. tuberculata* in which the most backward point tends to be rather high in the whorl, more or less at shoulder level. The collabral folds of *L. colombiana* tend to be more numerous and rather weaker than those of *L. tuberculata*.

L. colombiana is very similar to *L. eucosmia* (Pilsbry & Olsson), below. The two are provisionally treated as being distinct as the sculptural elements in *L. colombiana* appear to be considerably less regular, in both size and spacing, than in *L. eucosmia*, which, in addition. seems to be consistently smaller. In view of the synonymy given herein for *L. eucosmia*, it is felt that had these two nominal species occurred together, evidence of their close association might well lead one to conclude that they should be treated as no more than separate subspecies.

Longiverena eucosmia (Pilsbry & Olsson, 1935)

Figs 263–267

*v 1935 *Hemisinus (Longiverena) eucosmius* Pilsbry & Olsson: 13; pl. 3, fig. 2.
*v 1935 *Hemisinus (Longiverena) lapazanus* Pilsbry & Olsson: 13; pl. 3, figs 3, 4.
*v 1935 *Hemisinus (Longiverena) hopkinsi* Pilsbry & Olsson: 14; pl. 3, fig. 8.
*. 1935 *Hemisinus (Longiverena) laciranus* Pilsbry & Olsson: 14; pl. 3, fig. 5.
*. 1935 *Hemisinus (Longiverena) waringi* Pilsbry & Olsson: 14; pl. 3, fig. 9.
*v 1938 *Semisinus peyeri* de Greve: 104; pl. 4, figs 7–11.
*. 1941 *Hemisinus peyeri dickersoni* Palmer *in* Liddle & Palmer: 42; pl. 6, figs 15–18.
v. 1969 *Aylacostoma (Longiverena) eucosmius* (Pilsbry & Olsson) Parodiz: 146; pl. 16, figs 10, 11, 13.
v. 1969 *Aylacostoma (Longiverena) peyeri* (de Greve) Parodiz: 148.
. 1969 *Aylacostoma (Longiverena) waringi* (Pilsbry & Olsson) Parodiz: 148; pl. 16, fig. 1.
. 1969 *Aylacostoma (Longiverena) peyeri dickersoni* (Palmer) Parodiz: 149.
v 1982 *Aylacostoma dickersoni* (Palmer); Parodiz *in* Bristow & Parodiz: 48.

LECTOTYPE of *H. eucosmius* Pilsbry & Olsson, 1935, selected herein: ANSP 13088, shell figured Pilsbry & Olsson, pl. 3, fig. 2. Mugrosa Formation, Tertiary, Well 660, depth 1803–1815 feet. The two accompanying shells on the same core sample are paralectotypes.

Lectotype of *H. lapazanus* Pilsbry & Olsson, 1935, selected herein: ANSP 13090, original of their pl. 3, fig. 3. The original of their pl. 3, fig. 4 and two other shells are paralectotypes. All Mugrosa Formation, near El Centro, Square Mile 16S, 8E (O.C. Wheeler Colln).

Lectotype of *H. hopkinsi* Pilsbry & Olsson, 1935, selected herein: ANSP 13089, original of their pl. 3, fig. 8, same details as *H. lapazanus*. The accompanying specimen is a paralectotype.

Holotype of *S. peyeri* de Greve, PIMUZ 356, selected as 'typus' by him (1938: 105; pl. 4, figs 9, 11). PIMUZ 358, 359 and 360 are paratypes; all Late Caenozoic, Pebasian; Iquitos, Peru (Peyer Colln).

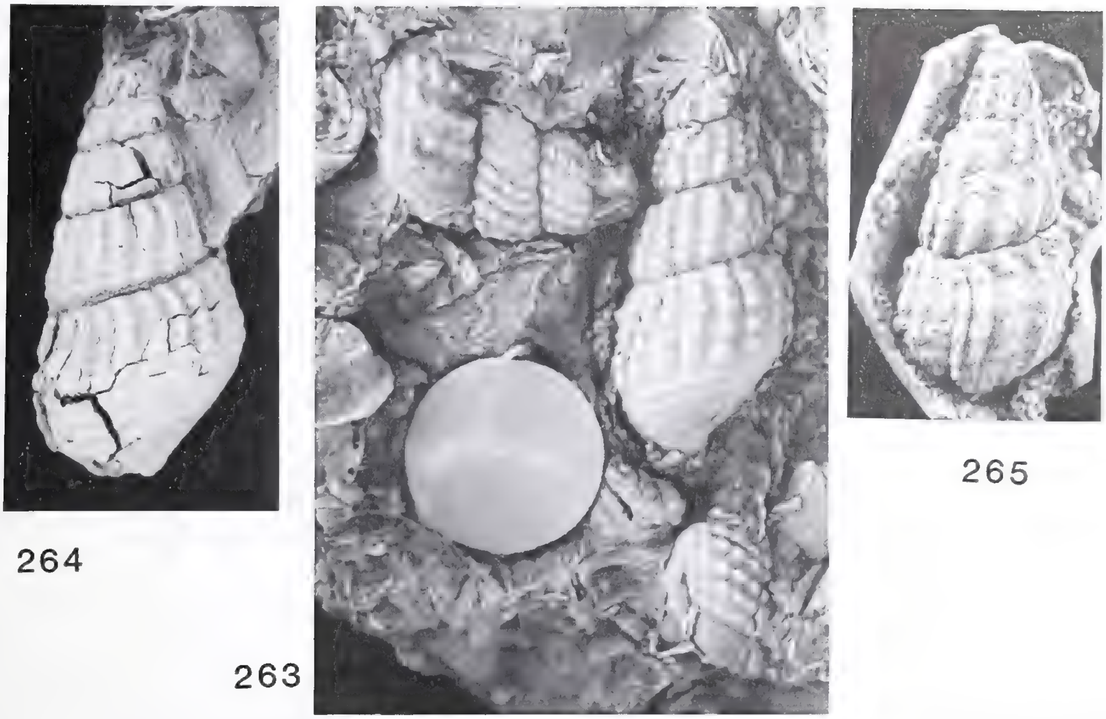
OTHER MATERIAL. BMPD GG19865, Loc. CRB1, Basal Azogues Formation, Miocene; Cuenca Basin, Ecuador (identified as *A. dickersoni* by Parodiz *in* Bristow & Parodiz, 1982: 48), has been studied.

FURTHER RECORDS. As *Hemisinus peyeri dickersoni* Palmer from its type locality (Liddle & Palmer, 1941: 36, map) = Loyola Formation (Miocene), southwest side of Cojitambo, Cuenca Basin, Ecuador (Bristow & Parodiz, 1982: 12, 48). As *Hemisinus (Longiverena) laciranus* Pilsbry & Olsson (1935), from La Cira Formation, Tertiary (Miocene), near La Cira, Colombia, ANSP 13078 (O.C. Wheeler Colln). As *Hemisinus (Longiverena) waringi* Pilsbry & Olsson (1935), from La Cira Formation, near Zopffs, ANSP 13072 (W.W. Waring Colln).

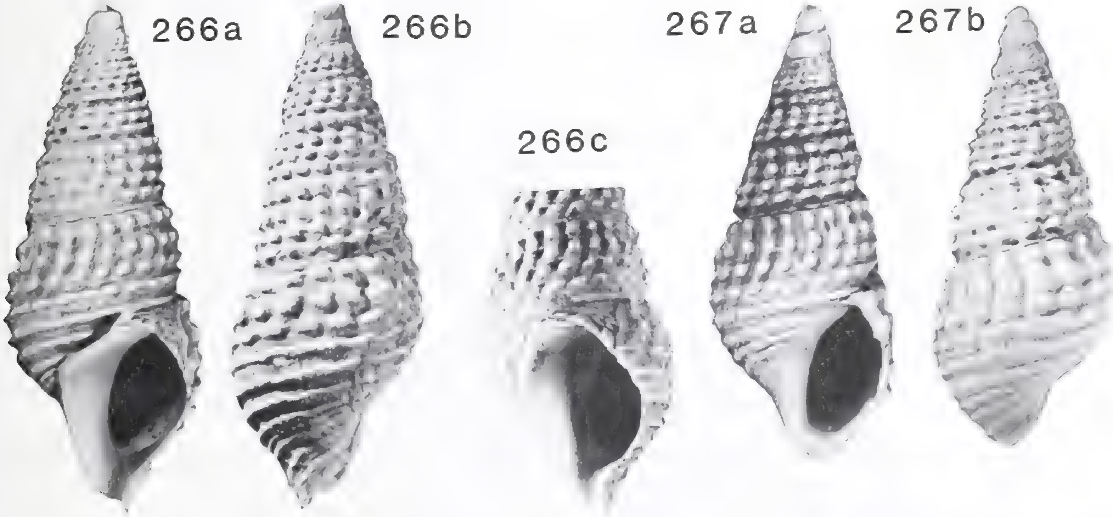
DISTRIBUTION. Miocene, Cuenca Basin, Ecuador; Mugrosa and La Cira Formations, Tertiary (? both Miocene), Magdalena Valley, Colombia; Late Caenozoic, Pebasian, Iquitos, Peru.

DIAGNOSIS. Small *Longiverena* with spire angle of about 30°; whorls biconvex; sculpture of three to five spiral ribs per whorl, expanded into strong, rather square tubercles where they cross the 9 – 18 opisthocyrt collabral folds per whorl; body whorl below periphery with up to about five spiral ribs, lacking collabral folding.

DESCRIPTION. The apex has never been seen. The best specimens are those described as *S. peyeri* de Greve from Iquitos; seven whorls are present in the holotype PIMUZ 356. The sculpture is first seen on its third whorl and is, by then, of adult character. The spiral sculpture consists of 3 – 5 ribs on each body whorl separated by interspaces of approximately



Figs 263–265 *Longiverena eucosmia* (Pilsbry & Olsson) and *L. eucosmia mugrosana* (Pilsbry & Olsson). **263**, ANSP 13088; bedding plane in borehole core with **lectotype** (selected herein) of *Hemisinus (Longiverena) eucosmius* Pilsbry & Olsson, figured by Pilsbry & Olsson (1935: pl. 3, fig. 2). Well 660, depth 1803–1815 feet, Middle Magdalena Valley, Colombia (the two accompanying and damaged paralectotypes were neither figured nor discussed by Pilsbry & Olsson); × 4. **264**, *Longiverena eucosmia mugrosana* (Pilsbry & Olsson), ASNP 13087; holotype of *Hemisinus (Longiverena) mugrosanus* Pilsbry & Olsson, figured by Pilsbry & Olsson (1935: pl. 3, fig. 1), Olsson & La Tour Colln; × 4. **265**, GG19865; latex cast of external mould, *L. eucosmia*; specimen recorded as *Aylacostoma dickersoni* (Palmer) by Bristow & Parodiz (1982: 48); Miocene, Basal Azogues Formation; Loc. CRB 1, Cuenca Basin, Ecuador; Bristow Colln; × 4.



Figs 266–267 *Longiverena eucosmia* (Pilsbry & Olsson). Specimens described as *Semisinus peyeri* de Greve; Pebasian; Iquitos, Peru; Peyer Colln. **266**, PIMUZ 356 ; holotype, figured by de Greve (1938: pl. 4, figs 9, 11). **267**, PIMUZ 358; paratype, figured by de Greve (1938: pl. 4, figs 8, 10). a, b, front, rear. All × 5.

the same width. The spacing of the ribs varies. In some specimens a definite subsutural ring is formed and sometimes there is a particularly wide gap between the topmost spiral and the one immediately below. The ribs are thickened into bosses where they cross the rather strong, sigmoid collabral folds, of which there are about eight on early whorls, increasing to 14 – 18 on later whorls. They decrease in strength below the periphery and normally die away by the lower suture so that the four or five spiral ribs on the lower half of the body whorl are devoid of collabral tuberculations. The aperture is not complete in any specimen either seen or figured elsewhere. The two best-preserved appear to be one of the syntypes (in ANSP) of *Hemisinus peyeri dickersoni* Palmer (*in* Liddle & Palmer 1941: pl. 6, fig. 16) and the

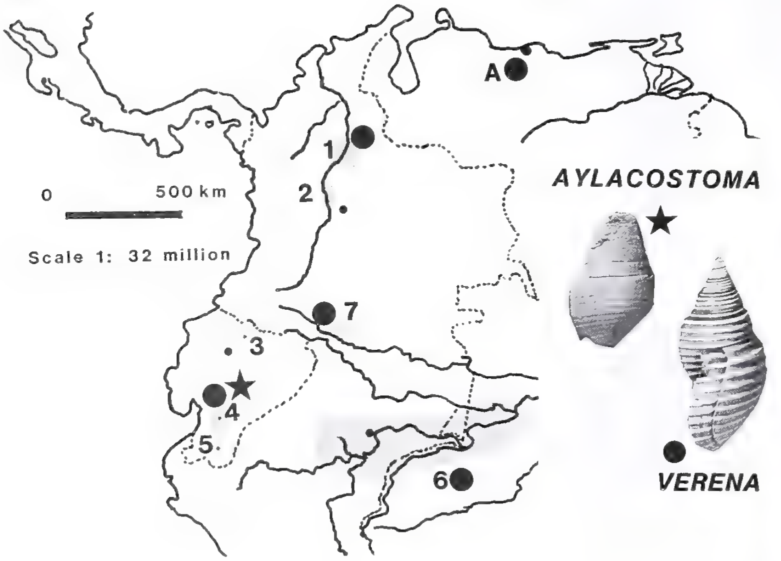


Fig. 268 Neogene distribution of *Verena* and *Aylacostoma*. Key as for Fig. 6 (p. 177). ●, *Verena*; ★, *Aylacostoma*. Inset: top left, *Aylacostoma* sp.; Miocene, Cuenca Basin, Ecuador; bottom right, *Verena browni* (Etheridge); Puerto Nariño, Colombia. Both × 2.

holotype of *Semisinus peyeri* de Greve (PIMUZ 356). The inner and outer lip meet adapically to form a moderately obtuse arch. The columellar and parietal callus pad has a definite rim on its left margin because it stands proud of the main shell surface. The base of the aperture is produced anteriorly in a way reminiscent of the pouring lip of a jug to form a basal notch.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
ANSP 13088, lectotype of *L. eucosmia*	*12.6	5.9	–	–	–
ANSP 13089, lectotype of *L. hopkinsi*	*15 (P&O)	–	–	–	28°
ANSP 13090, lectotype of *L. lapazana*	*14 (P&O)	–	–	–	30°
ANSP 13072, *L. waringi*, type illustration.	14 (P&O)	–	–	–	–
ANSP 13078, *L. lacirana*, type illustration	*11.5 (P&O)	–	–	–	–
PIMUZ 356, holotype of *L. peyeri*	13.2	5.2	5.4	2.54	28°
PIMUZ 358, paratype of *L. peyeri*	11.9	5.0	4.5	2.38	32°

(P&O) = Measurements from Pilsbry & Olsson (1935); * = decollated or other damage.

Note. Most of the specimens are too incomplete for meaningful measurements to be made. Measurements of spire angles are prone to error in the case of specimens partly embedded in matrix and are best omitted.

REMARKS. One of the important but less obvious features uniting the nominal species placed in synonymy here is that the spiral ribbing is not markedly dominant over the collabral folding as in *S. tuberculifera* (Conrad) and *S. coronata* (Etheridge), both of which occur at Iquitos with the present species. The apertural features given in the above description and the character of the ribbing are those of *Longiverena*. Parodiz (1969) synonymized the Colombian species *H. lapazanus*, *H. hopkinsi* and *H. laciranus* under the name *H. eucosmius*. His illustrations of the species are copies of Pilsbry & Olsson's originals: thus Parodiz pl. 16, fig. 10 = *hopkinsi*; fig. 11 = *lapazanus* (Pilsbry & Olsson's fig. 4); fig. 13 = *eucosmius*. He did not refigure *H. laciranus*. This synonymy is accepted here, and to avoid confusion the species remains described under the specific name *eucosmia* even though the best specimen is probably the lectotype of *H. hopkinsi* and, moreover, the type locality of *H. eucosmius*, being in a borehole, is not ideal. *H. laciranus* and *H. waringi*, from the La Cira Formation, are the only two of these five synonyms which are not confined to the underlying Mugrosa Formation. On *H. lacirana* the sculptural elements are weaker and more widely spaced than usual. However, they are essentially of the same type as seen in other specimens assigned to *L. eucosmia*. *H. waringi* from the La Cira Formation was based on an external mould (ANSP 13072) which is clearly not sagittal, and thus appears more acutely spired that it really is. It, too, is here accepted as a synonym of *L. eucosmia* on the character of its sculpture.

Hemisinus (Longiverena) mugrosanus Pilsbry & Olsson (1935: 13; pl. 3, fig. 1 – ANSP 13087) was also described from the Mugrosa Formation. It would seem to be closely related to these above-mentioned species but is here considered to be a distinct subspecies of *L. eucosmia* because its sculpture is not of spiral ribs but of spiral grooves cutting the collabral sigmoid folds.

Both the well-preserved *Semisinus peyeri* de Greve from Iquitos and the rather fragmentary *Hemisinus peyeri dickersoni* Palmer from the Cuenca Basin are assigned to *L. eucosmia* because of their virtually identical sculpture, whorl shape and profile. Pilsbry (1944: 146) and Parodiz (*in* Bristow & Parodiz 1982: 48) regarded both as being specifically distinct, but I cannot detect any appreciable differences between them. BMPD GG19865 from CRB 1 in the Cuenca Basin was identified as *A. dickersoni* by Parodiz. It is a single damaged external mould which shows sculpture typical of *L. eucosmia*.

The differences between *L. eucosmia* and the very similar *L. colombiana* are discussed under the latter, p. 250.

Genus **VERENA** H. & A. Adams, 1854

TYPE SPECIES. *Melanopsis crenocarina* S. Moricand, 1841. Recent, eastern Brazil (Bahia, Para). By monotypy (H. & A. Adams 1854: 308).

DIAGNOSIS. Comparatively stout Thiaridae with broad sloping ramp and angular shoulder; spire angle 35°–80°; aperture about half shell height; columella truncated above anterior notch as in *Hemisinus*; spiral ribbing strong; collabral sculpture weak or absent except for growth lines; aperture with weak sinus developed on ramp, outer lip prosocyrt; operculum not seen; presumed ovoviviparous (see under *V. crenocarina* (below), embryonic shells extracted from inside adult).

SPECIES ASSIGNED. Recent: The type species only. Fossil: *Hemisinus (Verena) crenocarina ava* Pilsbry & Olsson, 1935, = *Hemisinus (Verena) laevicarina* Pilsbry & Olsson, 1935, both ?Miocene, La Cira Formation, Colombia; *Ampullaria guaduasensis* Anderson, 1928, see p. 256; *Melanopsis? browni* Etheridge, 1879, Late Caenozoic, Pebasian, Canamá, Três Unidos, Puerto Nariño; *Verena* sp. (aff. *browni*, p. 258), Miocene, Mangán Formation, Cuenca Basin, Ecuador; *Verena lataguensis* sp. nov. (p. 258), Late Caenozoic, La Tagua, Colombia; *Hemisinus barloventoensis* Macsotay, 1968, Miocene, Cumaca and Siquire Formations, northern Venezuela.

DISTRIBUTION. Neogene and Recent, northern South America (Colombia, Ecuador, Peru, Brazil, Venezuela).

REMARKS. *Pyrgulifera* (Meek, 1877), a widespread Cretaceous to Eocene genus, is of similar shape but its columella reaches the abapical edge of the shell and is not truncated as in *Verena*. There is no reason, therefore, for thinking that the two genera are closely related. Parodiz (1969: 144–145) placed *Gonioconcha striata* Bonarelli (1927) and *Hypsipleura* (?) *bracklebushi* Bonarelli (1927), both from the Palaeocene of Argentina, in *Verena*. Their type illustrations suggest that some relationship with contemporaneous *Pyrgulifera* would be more likely than with later *Verena*. Parodiz (1969: 140) also tentatively placed *Hemisinus (Verena) avus* Pilsbry & Olsson in *Pyrgulifera*. Here, it is reassigned to *Verena* and is regarded as no more than a subspecies of *V. crenocarina*. The poorly preserved *Ampullaria guaduasensis* Anderson is also thought to be close to *V. crenocarina*. The other fossil species dealt with herein have more acute spires but are assigned to *Verena* because they possess the ramp, spiral sculpture, apertural features and growth lines typical of the genus.

Verena crenocarina (S. Moricand, 1841) Figs 269–272

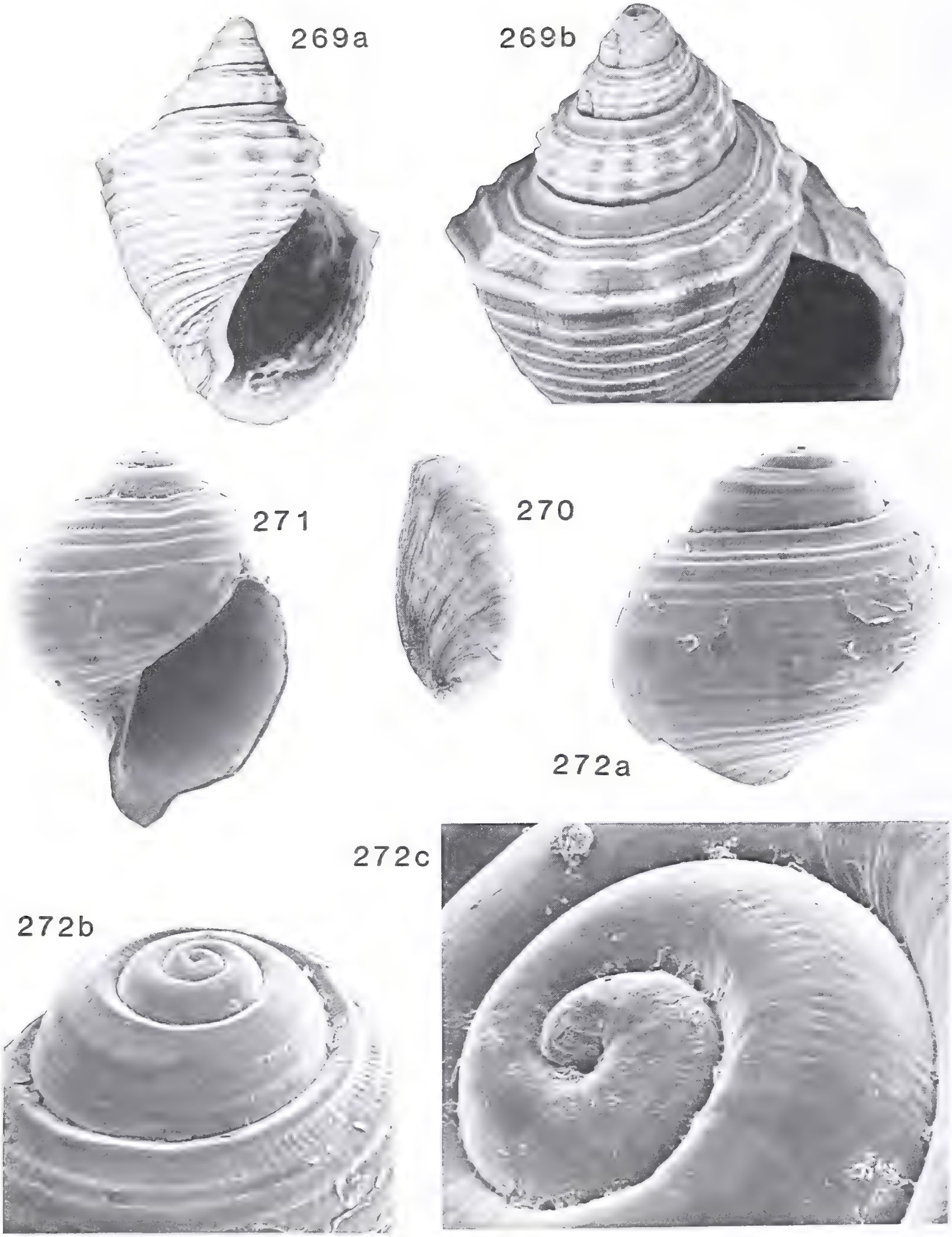
*	1841	*Melanopsis crenocarina* S. Moricand: 61; pl. 4, figs 10, 11.
*?	1844	*Melania cingulata* Jonas: 51.
.	1847	*Melania crenocarina* (Moricand) Philippi: 174; pl. 4, fig. 14.
.	1854	*Verena crenocarina* (Moricand) H. & A. Adams: 308.
.	1859	*Verena crenocarina* (Moricand); Chenu: 296, fig. 2055.
v.	1860	*Hemisinus crenocarina* (Moricand) Reeve: pl. 4, fig. 19.
.	1878	*Hemisinus crenocarina* (Moricand); Brot: 378; pl. 41, figs 4, 4a.
.	1902	*Hemisinus crenocarina* (Moricand); von Ihering: 667.
*?	1924	*Purpura woodwardi* Roxo: 49; pl. 1, figs C, C′, D.
.	1954	*Aylacostoma (Verena) crenocarina* (Moricand) Morrison: 377.
.	1967	*Aylacostoma (Verena) woodwardi* (Roxo) Santos & Castro: 414, figs 1–3.

MATERIAL STUDIED. All Recent, Brazil; 5 shells, Para (BMZD1984218); 3 shells, Brazil (BMZD 1984219); 3 shells (+ 2 embryonic shells extracted from adults, 1982), Brazil, Cuming Colln (BMZD1984220/1–5).

FURTHER RECORDS. Recent: type locality, Rio de Pedra Branca, Bahia Province, Brazil (Moricand, 1841). Fossil: Late Caenozoic, Pebasian; Três Unidos, Peruvian bank of Rio Javari (?Roxo, 1924; ? Santos & Castro, 1967).

DIAGNOSIS. Large stout *Verena* with spire angle of up to 80°; shoulder distinctly coronate; spiral sculpture of up to two ribs on ramp, two more below carina on spire whorls and 14 ribs on last whorl; collabral sculpture of about twelve folds per whorl; operculum filling two-thirds aperture.

DESCRIPTION. The shell is stout. The spire angle increases from about 60° to 80° with growth as the rather crenulate carina at the shoulder increases in strength. The apex is known only from two embryonic shells obtained by washing out an adult specimen (BMZD Cuming Colln). The apices of all adults are missing. The embryonic shells are ficiform and reminiscent of the genus *Tonna* both in shape and ribbing. The two earliest whorls are smooth and much broader than high. Up to four spiral ribs are developed by the third whorl. The adapical rib is strong and separated from the previous whorl by a canaliculate suture. The other ribs are weaker and more rounded. On the last whorl present in these embryonic shells, up to eight spiral ribs may occur: these die out below the periphery. The early whorls of adult shells are strongly convex with the periphery at their lower suture, and their ribbing pattern is basically similar to that on the preceding embryonic whorls. The canaliculate suture develops into a subsutural shelf which does not increase in strength with growth. The rib below it forms an incipient shoulder. This is the strongest and most angular of the spiral ribs and is separated from the suture by a concave interspace. Below this rib, three or four spiral bands are separated by narrow grooves. On later whorls, the second rib below the suture strengthens to form the carinate shoulder. Eventually, one or rarely two less prominent additional ribs are developed on the ramp. The (usually two) ribs below the shoulder become stronger and further apart. On the body whorl up to about 14 spiral ribs are present. Some are of secondary strength, but their arrangement appears haphazard, the common pattern of alternating primary and secondary ribs being absent. The collabral sculpture, consisting of 10 – 12 folds per whorl, is comparatively weak. It is strongest near the shoulder, thus making the spiral ribs crenulate, with the carina at the shoulder being the most strongly affected. A shallow sinus is present on the ramp: below the shoulder the growth lines are prosocyrt. The aperture is broad and notched below. The columellar callus is weak and the parietal callus above it is increasingly so. The aperture is smooth within except for impressions of the external spiral ribbing close to the mouth itself. The shell is covered with dark brown periostracum. The inside of the aperture may be brown, white, or in one case, is white with two brown bands. The operculum is present in only one BMZD shell, and fills two-thirds of the aperture.



Figs 269–272 *Verena crenocarina* (S. Moricand). Recent, Brazil. **269**, BMZD 1984218; Para, history unknown. a, front, × 2; b, oblique view showing sculpture, × 4. **270**, BMZD 1903.2.4.1784; operculum; × 3. **271**, BMZD 1984220/2; embryonic shell extracted from an unfigured specimen (BMZD 1984220/1) in the Cuming Colln sample which contains the shell figured by Reeve (1860: pl. 4, fig. 16); front, × 20. **272**, BMZD 1984220/3; second embryonic shell extracted from same Cuming Colln sample. a, rear, × 20; b, oblique view of apex and early spire whorls, × 30; c, oblique view of apex, × 100.

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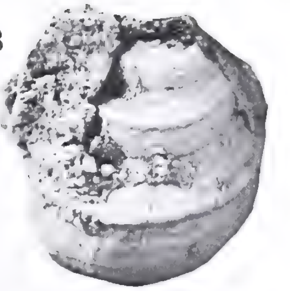

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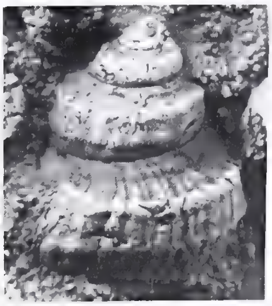

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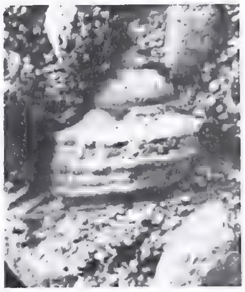

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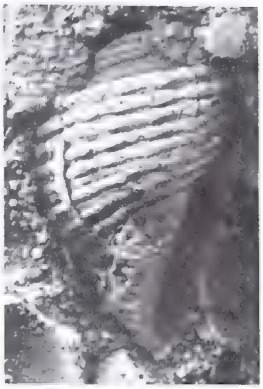


Figs 273–276 *Verena crenocarina ava* (Pilsbry & Olsson). La Cira Formation, probably Miocene; Middle Magdalena Valley, Colombia. **273**, ANSP 13079a, **lectotype** (herein selected) of *Hemisinus (Verena) laevicarina* Pilsbry & Olsson; oblique view of spire with shell axis rotated through about 90° anticlockwise compared with Pilsbry & Olsson (1935: pl. 3, fig. 10); Rio Oponcito, near Guanabanus; × 3. **274–276**, ANSP, unregistered; casts of external moulds in decalcified mudstone of *Hemisinus (Verena) ava* Pilsbry & Olsson, from type locality, near Zopffs; × 3.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
BMZD, Para	*34.6	26.7	23.5	–	–
BMZD, Para	*35.2	25.4	23.0	–	–
BMZD, Para	31.2	22.9	22.9	1.36	78°
BMZD, Cuming Colln.	22.1	15.7	15.7	1.41	–

* = decollated or otherwise extensively damaged.

REMARKS. *Verena crenocarina* (S. Moricand) is not only the type but also the only living species known of the genus. The illustrations (Roxo 1924, Santos & Castro 1967) of *Purpura woodwardi* suggest that it is conspecific with *V. crenocarina*, and there can be no doubt it was correctly assigned to *Verena* by Santos & Castro. The relationship between *V. crenocarina, s.str.* and *V. crenocarina ava* (Pilsbry & Olsson) is discussed under the latter, below. *V. guaduasensis* (Anderson) (p. 256) is also very similar to both these subspecies. Other fossil species of *Verena* are all more acicular.

Verena crenocarina ava (Pilsbry & Olsson, 1935)

Figs 273–276

- *v. 1935 *Hemisinus (Verena) avus* Pilsbry & Olsson: 15; pl. 3, figs 6, 7.
- *v 1935 *Hemisinus (Verena) laevicarina* Pilsbry & Olsson: 15; pl. 3, figs 10–12.
- . 1969 ? *Pyrgulifera avus* (Pilsbry) [*sic*] Parodiz: 140; pl. 15, figs 8, 9.
- . 1969 *Aylacostoma (Verena) laevicarina* (Pilsbry & Olsson) Parodiz: 145; pl. 15, figs 13, 14.

LECTOTYPE of *H. (V.) avus*, selected herein: ANSP 13071a, original of Pilsbry & Olsson (1935: pl. 3, fig. 7), a broken mould in decalcified mudstone, ? Miocene, La Cira Formation, near Zopffs, La Cira District, Colombia (W. Waring Colln). Numerous broken moulds ANSP 13071, with *Doryssa* and *Pachydon* in decalcified mudstone, are paralectotypes: they include the specimen described by Pilsbry & Olsson (1935: 15) as an aberrant form and figured by them (pl. 3, fig. 6). Details as for lectotype. The lectotype of *H. (V.) laevicarina*, selected herein, is ANSP 13079a, the original of Pilsbry & Olsson (1935: pl. 3, fig. 10), ? Miocene, La Cira Formation, Rio Oponcito near Guanabanus, Colombia (A. A. Olsson & E. La Tour Colln). The two shells ANSP 13079, figured by Pilsbry & Olsson (1935: pl. 3, figs 11, 12), are paralectotypes. No other material.

DISTRIBUTION. ?Miocene, La Cira Formation, Colombia only.

DIAGNOSIS. Like *V. crenocarina crenocarina*, but smaller, and lacking strong crenulations on the carinate shoulder, with less concave ramp, and slightly more acute spire with spire angle of 65°–70°.

DESCRIPTION. The early whorls are convex; the carinate shoulder and concave ramp above it develop later, as in *V. crenocarina, s.str.* (S. Moricand). The spiral sculpture is variable. The illustration of the lectotype of *V. crenocarina ava* (Pilsbry & Olsson 1935: pl. 3, fig. 7) shows three strong spiral ribs on the spire whorls and ten on the body whorl, separated by wide interspaces. On other moulds it appears to consist of rather broad convex bands separated by fairly narrow interspaces. The collabral sculpture is comprised of up to twenty folds per whorl. These appear to be formed by the bunching of the growth lines.

DIMENSIONS. In mm.	h	br	sa
Lectotype of *V. crenocarina ava*, ANSP 13071a	12.0	7	70°
Lectotype of *V. laevicarina*, ANSP 13079a	17.5	11	65°

Note. Dimensions of these incomplete specimens are from Pilsbry & Olsson (1935), and were apparently quoted to the nearest 0.5 mm. The spire angles are from their illustrations.

REMARKS. Neither Pilsbry & Olsson's (1935) text nor their extensively retouched and cut-out illustrations suggest that the type material of *Hemisinus (Verena) avus* consists of numerous broken moulds associated with *Longiverena* and *Pachydon* in blocks of decalcified mudstone.

Parodiz (1969: 140) tentatively assigned this species to *Pyrgulifera* but re-examination of this material establishes that the original placement of it in *Verena* was correct. *V. laevicarina* from the same formation appears to be synonymous. Its type material consists of worn, semi-decorticated, shells in a coarse sandstone. The very strongly carinate shoulder appears to be a preservational feature and traces of spiral ribbing typical of *Verena* may be seen on these specimens. None of the available specimens of *V. crenocarina ava* attains the size of the very similar living *V. crenocarina, s.str.* Several apparent differences such as spire angle and whorl profile are features which appear to change with growth. At present the two are treated as being distinct, with *V. crenocarina, s. str.* being distinguished by its less crenulate carina at the shoulder.

Verena guaduasensis (Anderson, 1928) Fig. 277

*v 1928 *Ampullaria guaduasensis* Anderson: 23; pl. 1, figs 19, 20.
. 1977 *Pomacea quaduasensis* (Anderson) [*sic*] Boss & Parodiz: 109.

HOLOTYPE. CAS 2721, 'Eocene ... Guaduas Beds, near San Juan de Rio Seco, upper valley of Rio Magdalena' (Anderson 1928). This is probably Santa Teresa Formation of late Oligocene to early Miocene age, possibly at km 106, Cambao to Bogotá highway (Butler 1939, 1942; Porta 1966). No other material.

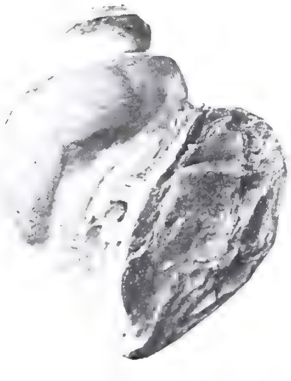


Fig. 277 *Verena guaduasensis* (Anderson). CAS 2721, internal mould; holotype of *Ampullaria guaduasensis* Anderson, figured by Anderson (1928: pl. 1, figs 19, 20), originally described as being from the supposedly Eocene Guaduas Beds from near San Juan de Rio Seco, but probably from the late Oligocene or early Miocene Santa Teresa Formation at km 106 on the Cambao to Bogotá Highway. Front, × 2.5.

DIMENSIONS. h, 20.6 mm; br, 15.1 mm; sa, *c*. 80°.

REMARKS. The unique holotype is an internal mould to which some shell material still adheres. Its shape and apertural features justify its assignment to *Verena*, and it may indeed belong to either *V. crenocarina, s.str.* (S. Moricand) or its subspecies *V. crenocarina ava* (Pilsbry & Olsson), although no decision can be reached in the absence of any details of shell sculpture. The age was given as Eocene by Anderson, but is here redated as probably Miocene, or at the earliest, late Oligocene. Boss & Parodiz (1977: 109) placed this species in *Pomacea*, a member of the Ampullariidae, and suggested that the age might be Pleistocene. Both this reidentification and their age determination appear to be completely without justification.

Verena browni (Etheridge, 1879) Figs 278–282

* 1879 *Melanopsis? browni* Etheridge: 87; pl. 7, fig. 4.
. 1924 *Melanopsis? browni* Etheridge; Roxo: 46.
. 1969 *Aylacostoma sulcatus* (Conrad) Parodiz: 141 (*pars*); pl. 14, figs 6, 7.
. 1981 *Aylacostoma (Aylacostoma) browni* (Etheridge) Costa: 644; pl. 1, figs 11, 12.

TYPE MATERIAL. Described by Etheridge from the Late Caenozoic, Pebasian, Canamá. Whereabouts of specimens unknown.

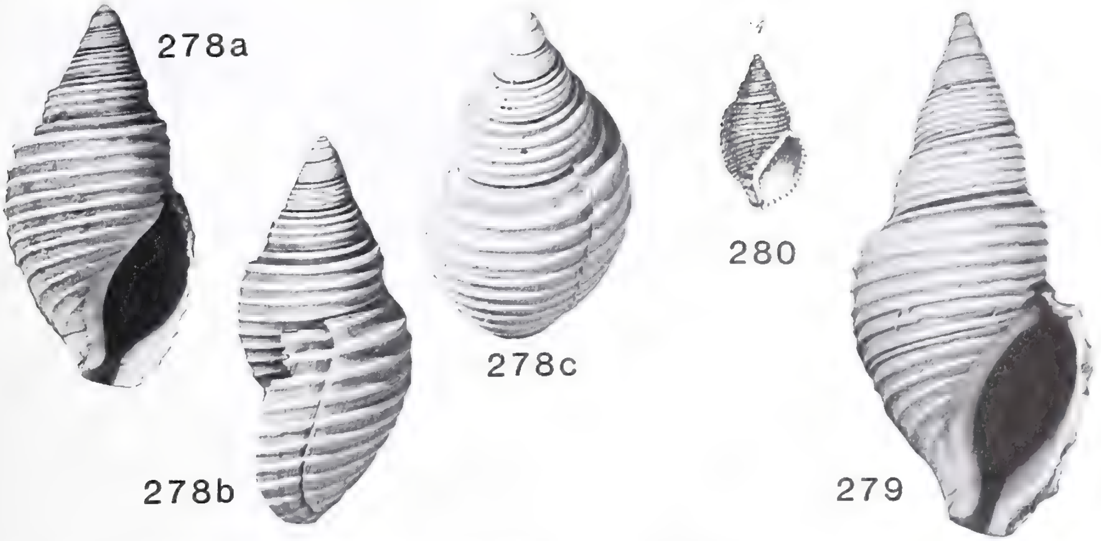
MATERIAL. BMPD GG19895–9, GG19916–7 (about fifty shells), Late Caenozoic, Pebasian; Puerto Nariño (Weeda Colln); studied. Otherwise recorded from Pebasian of Canamá (Etheridge 1879) and of Três Unidos (Roxo 1924, Parodiz 1969, Costa 1981). Late Caenozoic, Pebasian only; Upper Amazon Basin, Peru, Colombia.

DIAGNOSIS. Narrow *Verena* up to 25 mm high; spire angle 45°–55°; ramp, not very prominent, bordered by strong subsutural cord and another on shoulder; about three further strong cords visible on spire whorls and up to ten on final whorl; collabral sculpture lacking except for growth lines.

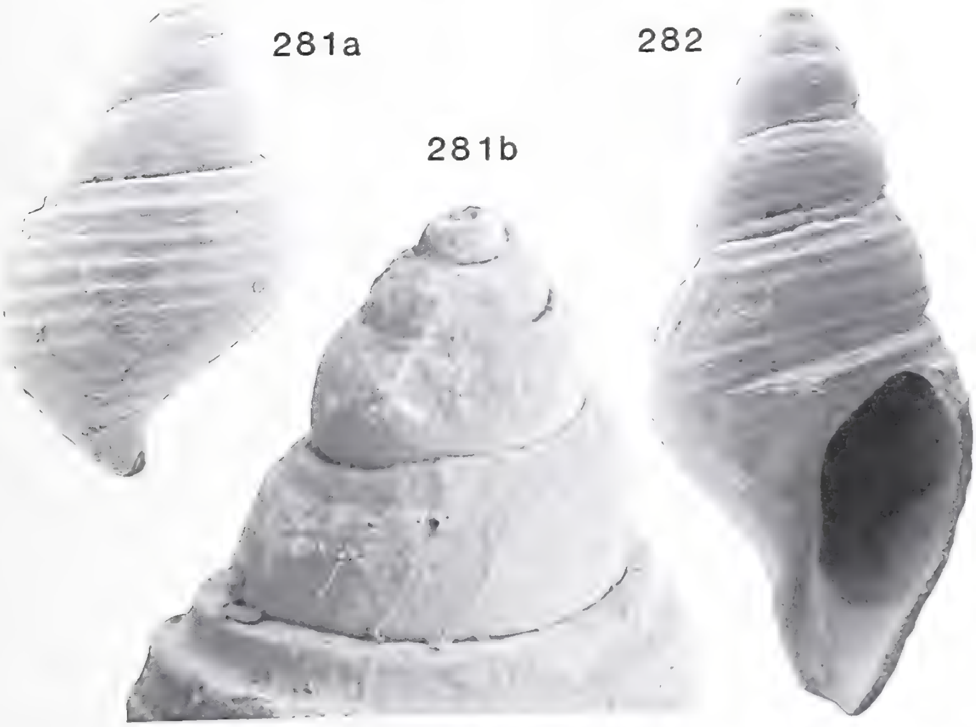
DESCRIPTION. There are up to ten convex whorls whose peripheries lie at, or just above, the suture. The concave ramp first appears on the fourth or fifth whorl and is not prominent until at least two whorls later. Its slope varies from almost horizontal to about 20° from the vertical. The first three or four whorls form a smooth apex ornamented only by strongly opisthocyrt–opisthocline growth lines. For the first whorl or so, the apex is almost planorbiform as in the living species of Hemisininae examined herein.

Spiral sculpture first appears on the third or fourth whorl as grooving. Within a whorl or so, the grooves become broader than the intervening cords and the adult sculptural pattern comes into being. The cords are rounded in section. The subsutural cord is of variable strength and juts out from the suture to give the ramp a stepped appearance. The strongest cord is that at the shoulder. Rare secondary spirals occur in some specimens. Very weak spiral striae may be seen, forming a reticulate pattern with the stronger growth lines. The growth lines are strongly prosocyrt except for a sinus developed below the suture. This leads those on early whorls, in particular, to be weakly sinusigeral in appearance. The aperture is typical of the genus and is virtually smooth within, with columellar callus obscuring nearly all traces of spiral sculpture. A definite posterior channelling or notch is developed.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Etheridge 1879: pl. 7, fig. 4.	19.5	12.5	11.4	1.56	50°
Parodiz 1969: pl. 14, fig. 6.	22.8	12.4	14.0	1.84	60°
Costa 1981: pl 1, fig. 11.	–	–	–	2.15	47°
GG19917	23.0	10.2	10.2	2.24	43°
GG19895	12.9	6.3	6.3	2.04	47°



Figs 278–280 *Verena browni* (Etheridge). Pebasian. **278**, GG19895; Puerto Nariño, Colombia; Weeda Colln. a, b, c, front, side, and oblique views, all × 4. **279**, GG19917; same details as Fig. 278; front, × 4. **280**, copy at original size of Etheridge's type illustration (1879: pl. 7, fig. 4); Canamá, Peru. Magnification not exactly known.



Figs 281–282 *Verena browni* (Etheridge). Pebasian; Puerto Nariño, Colombia; Weeda Colln. **281**, GG19916; a, rear, × 20; b, slightly oblique view of early spire whorls and apex, × 40. **282**, GG19986; front, × 20.

Remarks. Etheridge's type material from Canamá was never among those specimens presented to the BM by him and registered in 1879. As the original illustration is poor and the present material does not come from the type locality, it seems inadvisable to select a neotype. Some doubt as to the correctness of the present identification must remain as rather similar species occur at La Tagua (*V. lataguensis* sp. nov., p. 258) and in the Cuenca Basin (herein determined as *V.* sp. aff. *browni*). Furthermore, Etheridge's rather poor illustration is of a comparatively stout shell (see dimensions). The fact that Canamá lies in the same general area as Três Unidos and Puerto Nariño may be taken as evidence in favour of the determination being correct.

The newly collected material from Puerto Nariño is clearly conspecific with the shell figured by Parodiz (1969) as *Aylocostoma sulcatus* Conrad from Três Unidos. Parodiz later (Bristow & Parodiz 1982: 49) recognized that the Três Unidos material, referred to by Roxo (1924) and independently redescribed by Costa (1981), belonged to *browni* rather than *sulcatus*.

Parodiz also (Brown & Parodiz 1982: 48) reidentified as *Aylacostoma browni* specimens figured by de Greve (1938: pl. 4, fig. 18 and text-fig. 19) as *Semisinus sulcatus* (Conrad). De Greve's text-fig. 19 is of *Liris tuberculata* de Greve whilst his pl. 4, fig. 18 is herein reassigned to the living *Hemisinus kochi* (Bernardi 1856): see p. 240.

Material from the Cuenca Basin identified by Parodiz (*in* Bristow & Parodiz 1982: 48) as *Aylacostoma browni* is herein identified as *Verena* sp. aff. *browni*. The distinctions between *V. browni* and *V. lataguensis* sp. nov. are dealt with under the latter.

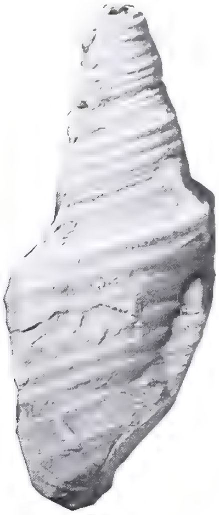


Fig. 283 *Verena* aff. *browni* (Etheridge). Miocene, Mangán Formation; Loc. CRB 42c, Cuenca Basin, Ecuador; Bristow Colln; rear, × 3.

Verena sp. aff. *browni* Fig. 283

v 1982 *Aylacostoma browni* (Etheridge); Parodiz *in* Bristow & Parodiz: 48, fig. 22.

MATERIAL. All Mangán Formation, Miocene, Cuenca Basin, Ecuador: BMPD GG19867/1–4, Loc CRB 42c; GG19868/1–2, Loc. CRB 36a; studied. Other material in Carnegie Museum, CM 46804 (20 specimens), CRB 42 (as above) (Bristow & Parodiz 1982: 49).

REMARKS. Parodiz identified the material both in Carnegie Museum and BMPD as *A. browni* and this is presumably the source of the identifications in faunal lists given in Bristow & Parodiz (1982: 10, 14). Several of these records, however, are not given in their systematic account (1982: 48–49). Neither the material in BMPD studied herein nor Parodiz' fig. 22 are of true *V. browni*. They are of a species with variable but generally lighter spiral sculpture and with a broader ramp. It also lacks the strong spiral rib which forms a subsutural collar in *V. browni*. One BMPD specimen, GG19869, may be the source of their record (1982: 10) of the species from the Loyola Formation (CRB 18b); it is very poorly preserved but does not appear to be a *Verena*.

Verena lataguensis sp. nov. Figs 284–285

HOLOTYPE. GG19920, Late Caenozoic; CAE 33/480–560 cm, La Tagua (Eden Colln). G19921–2, same data, and GG19923, CAE 33/560 cm, are paratypes.

NAME. From locality of La Tagua.

DIAGNOSIS. Small aciculate *Verena* with spire angle of about 35°; narrow concave ramp present; delicate spiral sculpture of six to eight sharp ribs below angular shoulder on spire whorls and between twelve and twenty ribs present on final whorl. Collabral sculpture lacking.

DESCRIPTION. All the specimens are incomplete and partly crushed. Examination of GG19922, the only shell with early whorls present, suggests that a complete adult would be of nine to ten whorls. A subsutural collar is of variable strength but never prominent. The ramp is otherwise smooth, narrow and strongly concave. The carina at the shoulder is no stronger than other spiral ribs. Below the shoulder there are 6 – 8 spiral ribs on spire whorls, and 12 – 20 on the final whorl. The ribs are always fine but are separated by interspaces which vary from about as thick as one rib (in the holotype) to over twice as wide (in paratype GG19921). Collabral sculpture is absent except for growth lines. These are typical of *Verena*, with a sinus developed on the ramp and of prosocyrt form below the shoulder. The apertures of all specimens are damaged. In the holotype weak callus is developed along the entire length of the aperture.

DIMENSIONS. In mm.	h	br	hap	hbw	sa
Holotype, GG19920	9.0	5.3	4.6	7.4	*c*. 35°
Paratype, GG19921	9.1	6.0	5.8	8.8	–

Note. The above dimensions (h, hbw) indicate that little of the shell above the body whorl is present in these specimens. Spire angle measurement is only meaningful in the case of the holotype.

REMARKS. This species differs from *V. browni* Etheridge in being smaller and in having much finer and more numerous spiral ribs. It also appears to have a more acute apical angle. It is also similar to *Verena* sp. aff. *browni* from the Cuenca Basin. This is also rather acicular but has fewer and stronger ribs. The other known species of *Verena* all have much stouter shells.

Hemisinus barloventoensis Macsotay (1968: 301; pl. 1, figs 6, 7, 9, 10) from the Miocene of Venezuela is very similar. It may be distinguished, however, by its much more noticeable ramp, which accounts for nearly half the height of the spire whorls. This gives its shell a distinctly turreted, or stepped, appearance.

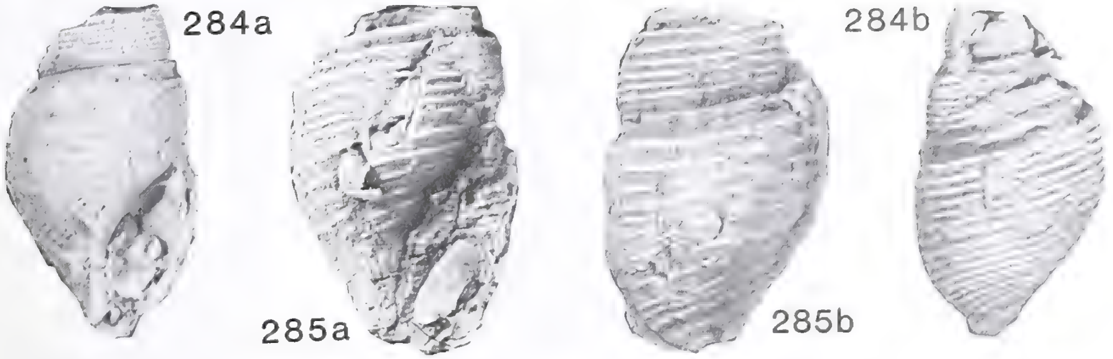
Genus *AYLACOSTOMA* Spix, 1827

[= *Aulacostoma* Agassiz, 1846: 10, unjustified emendation; no species mentioned].

TYPE SPECIES. *Aylacostoma glabrum* Spix, 1827, by subsequent designation of Morrison (1954: 376). Recent, Brazil.

DIAGNOSIS. Acicular, with pronounced ramp and shoulder developed on last whorl or so; spiral sculpture weak, mainly of grooving tending to be concentrated on ramp; collabral sculpture virtually absent; aperture notched below; operculum auriculate, approximately half whorl of rapidly expanding spiral.

OTHER SPECIES ASSIGNED. Fossil: *Aylacostoma* sp., Mangán Formation, Miocene; Ecuador; see p. 261. Distribution Neogene and Recent, northern and central South America.



Figs 284–285 *Verena lataguensis* sp. nov. Late Caenozoic; Loc. 33/480–560, La Tagua, Colombia; Eden Colln. **284**, GG19920, **holotype**; a, b, front, rear, × 5. **285**, GG19921, paratype; a, b, front, rear, × 5.

REMARKS. Morrison's designation of the type species (1954: 376) was: 'Genotype: (*Aylacostoma glabrum* Spix)= *Aylacostoma (Aylacostoma) scalare* (Wagner) 1827'. Parodiz (1969: 141) follows this almost exactly but attributes the designation to Morrison (1952): this is an abstract of a meeting report which I have not seen and may be invalid. A previous type designation by Cossmann (1909: 126) was: 'Genotype *Aulacostoma scalaris* Spix'. This is not accepted here as valid because *scalaris* – a Wagner name – was not one of the species names originally used in conjunction with *Aylacostoma*. In any case *Melania scalaris* Wagner is here regarded as a junior objective synonym of *Aylacostoma glabrum* Spix. Similar treatment is accorded herein to all other new names proposed by Wagner (1827) for species named by Spix in the illustrations of their joint work.

Aylacostoma and *Aulacostoma* were placed in the synonymy of *Hemisinus* Swainson, 1840, by both Thiele (1929: 201) and Wenz (1939: 718). As *Aylacostoma* is valid and has priority over *Hemisinus*, such an arrangement is unacceptable. One other species, *Aylacostoma tuberculata* Spix, was originally assigned to the genus, and is the type species of *Longiverena* Pilsbry & Olsson 1935 (see p. 246). Adams & Adams (1854: 291) listed nine living species, including *A. scalare* but not *A. tuberculata*, as belonging to *Aylacostoma*. In spite of this, the type species is probably the only living representative of the genus.

Aylacostoma glabrum Spix, 1827 Figs 286–291

*v 1827 *Aylacostoma glabrum* Spix: pl. 8, fig. 5.
*v 1827 *Melania scalaris* Wagner: 15.
. 1854 *Aylacostoma scalaris* (Wagner) H.&A. Adams: 299.
. 1859 *Aylacostoma scalaris* (Wagner); Chenu: 289, fig. 1966.
*v 1860 *Hemisinus behni* Reeve: pl. 2, figs 8a–f.
*v 1860 *Hemisinus tenuilabris* (*ex* Behn MS) Reeve: pl. 5, figs 22a, b.
. 1878 *Hemisinus brasiliensis* (Moricand); Brot: 392 (*pars*: 'var.' = *Melania scalaris* Wagner).
. 1878 *Hemisinus behni* Reeve; Brot: 383; pl. 39, figs 12, 12a–c.
. 1878 *Hemisinus tenuilabris* Behn (= Reeve); Brot: 384; pl. 40, figs 1, 1a.
. 1902 *Hemisinus behni* Reeve; von Ihering: 674.
. 1902 *Hemisinus tenuilabris* Reeve; von Ihering: 688, fig. 4.
. 1902 *Hemisinus tenuilabris* Reeve 'var. nov.' *araguayana* von Ihering: 669, fig. 5.
. 1954 *Aylacostoma (s.str.) glabrum* Spix = *scalare* (Wagner); Morrison: 376.
. 1983*a* *Aylacostoma glabrum* Spix = *Melania scalaris* Wagner; Fechter: 222.

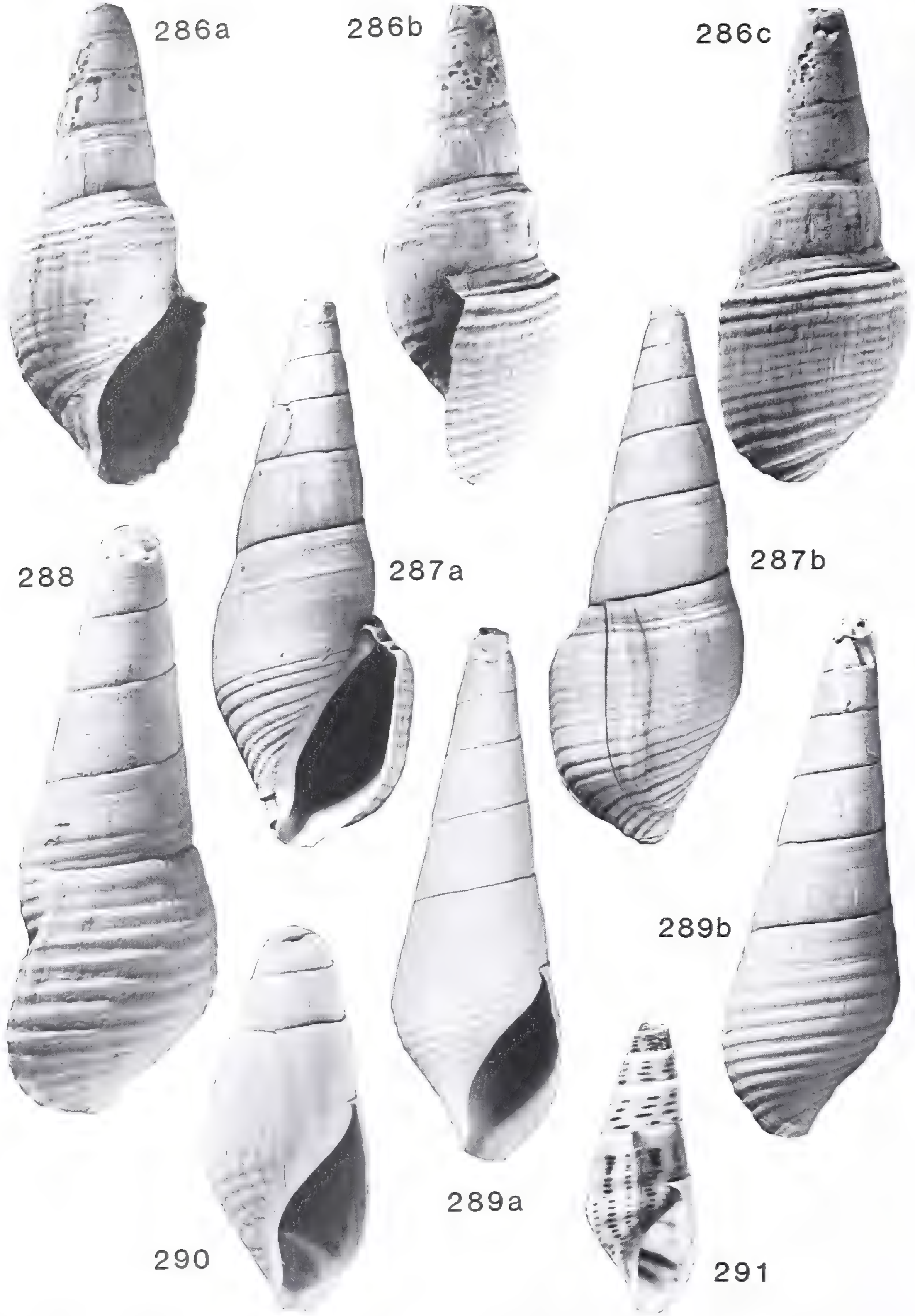
HOLOTYPE of *Aylacostoma glabrum* Spix, = holotype of *A. scalaris* (Wagner), Zool. Staatsmus. München, figured Spix (1827). Recent, Mandiocca, St Sebastian Province, Brazil. Also studied: the lectotype of *Hemisinus behni* Reeve, selected herein, figured Reeve 1860: pl. 2, figs 8a, b. The two accompanying shells (pl. 2, figs 8c, d, e, f) are paralectotypes. All Recent, Pernambuco, Brazil (Cuming Colln, BMZD 1984221). Also the lectotype of *H. tenuilabris* Reeve, selected herein, figured Reeve 1860: pl. 5, figs 22a, b; the two accompanying shells are paralectotypes. All Recent, Brazil (BMZD 1984222). Also 15 shells from Recent of Rio Grande Franca, São Paulo Province, Brazil, identified by von Ihering (1902) as belonging to three 'varieties' of *H. tenuilabris* 'Behn' (BMZD 1903.12.5.1–15).

DISTRIBUTION. Recent, eastern Brazil only.

DIAGNOSIS. *Aylacostoma* with tall straight-sided spire. Ramp and shoulder variable, developed only on whorls more than 25 mm below apex. Apical angle of spire whorls 25°, increasing to about 30° by final whorl. Spiral sculpture developed on later whorls only, otherwise almost smooth except for subsutural grooving and slight bunching of growth lines; growth lines only slightly sinuate.

DESCRIPTION. All the specimens are decollated. Up to five spire whorls are almost straight-sided, having very weakly incised sutures. The final whorl and sometimes part of the penultimate whorl is variable. It may be strongly shouldered with a marked ramp, as in the holotype of *A. glabrum*, the lectotype of *A. behni* and some of the BMZD specimens identified as *H. tenuilabris* 'var.' by von Ihering. In other specimens, including the type series of *Hemisinus tenuilabris* Reeve, it remains almost straight-sided above the periphery. Intermediates exist between these two extremes. The early whorls are virtually smooth except for weakly opisthocyrt growth lines which tend to become bunched, as on the body whorl of the holotype of *A. glabrum* itself.

Spiral sculpture varies considerably. Grooves separate rather broad, convex bands on the body whorl of large specimens, with the strongest sculpture occurring below the periphery. Comparatively small specimens, including the type



Figs 286–291 *Aylacostoma glabrum* Spix. Recent, Brazil. **286**, holotype in Zool. Staatsmus. München; figured by Spix (1827: pl. 8, fig. 5); Mandiocca, St Sebastian Province. a, b, c, front, side, rear, all × 2.5. **287–289**, *Hemisinus behni* Reeve. Pernambuco (= Recife); Cuming Colln. **287**, BMZD 1984221; **lectotype** (selected herein), figured by Reeve (1860: pl. 2, figs 8a, b). a, b, front, rear, × 2. **288**, BMZD 1984221; paralectotype, figured by Reeve (1860: pl. 2, figs 8c, d); side, × 2. **289**, BMZD 1984221; paralectotype, figured by Reeve (1860: pl. 2, figs 8e, f). a, b, front, rear, × 2. **290**, BMZD 1984222; **lectotype** (selected herein) of *Hemisinus tenuilabris* Reeve, figured by Reeve (1860: pl. 5, figs 22a, b); Brazil; Cuming Colln; front, × 2. **291**, BMZD 1903.12.5.7; small shell of '*H. tenuilabris* Reeve' with periostracum removed with bleach to show colour patterning; Saō Paulo, from H. von Ihering; front, × 2.

series of *Hemisinus tenuilabris* Reeve, are virtually smooth except for this last feature. The growth lines remain weakly sinuate even on the body whorl and no proper sinus is developed in the region of the ramp. Callus on the inner lip is comparatively weak, even in the largest specimens. The basal apertural notch is easily seen.

Two opercula were found loose with the three shells in the type series of *H. behni* Reeve. They are both about 11 mm high and 5 mm broad, and presumably belonged to shells whose apertures measured about 18 × 9 mm.

DIMENSIONS. In mm.	h	br	hap	hbw	h/br	eh/br	sa
Holotype of *A. glabrum* Spix	*30.6	12.8	12.4	18.6	2.4	3.0	24°–30°
Lectotype of *A. behni* Reeve	*45.8	16.9	18.7	28.5	2.7	2.8	25°–28°
Lectotype of *A. tenuilabris* Reeve	*29.8	13.8	17.4	23.0	2.2	2.9	22°

* = decollated or otherwise badly damaged.

REMARKS. Sample BMZD 1903.12.5.1–15, identified by von Ihering, contains shells resembling the types of all three nominal species included in this synonymy. Brot's (1878: 392) placement of *Melania scalaris* Wagner and *A. glabrum* Spix in the synonymy of *Hemisinus brasiliensis* Moricand is without foundation. His illustrations (1878: pl. 40, fig. 12, 12a–c) of *H. brasiliensis* are correctly identified, but none of his illustrations are of shells resembling *A. glabrum*.

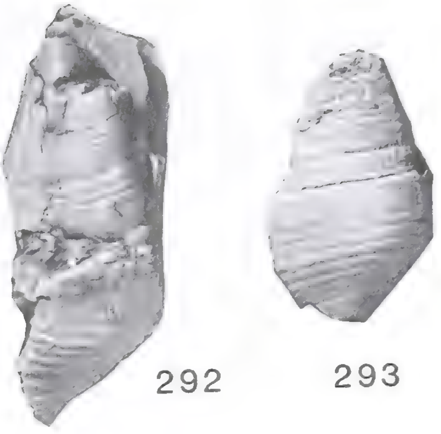
Aylacostoma sp. Figs 292–293

v 1982 *Aylacostoma* sp. Bristow & Parodiz: 49.

MATERIAL STUDIED. BMPD GG19866/1–3, CRB 42, Miocene, Mangán Formation; Cuenca Basin, Ecuador. No other record.

DESCRIPTION. Because of crushing and other damage the apical angle cannot be measured properly, but it probably lies between 30° and 35° in this rather acicular species. Both GG19866/2 and the reverse side of GG19866/1 show the ramp and semi-angular shoulder typical of *Aylacostoma*. The spiral sculpture is variable and consists of grooves with rather wide interspaces. On GG19866/1 the grooving is concentrated on the ramp and on the neck region of the body whorl, and is absent from the peripheral region. On GG19866/2, grooving is absent only from the ramp. GG19866/3 differs from GG19866/1 in that spiral grooving is developed on the periphery of the last whorl although absent from the peripheral region of spire whorls. Collabral sculpture is absent except for growth lines which are moderately sinuous with only a very weak sinus developed on the ramp. The only apertural features which can be made out are the columellar callus and indications, from the growth lines, of the presence of a basal notch.

DIMENSIONS. In mm.	h	eh	br	sa
GG19866/1	22.6	30.0	9.5	–
GG19866/2 (laterally crushed)	18.3	23.5	11.2	–



Figs 292–293 *Aylacostoma* sp. Miocene, Mangán Formation; Loc. CRB 42, Cuenca Basin, Ecuador; Bristow Colln. **292**, GG19866/1. **293**, GG19866/2. Both × 2.

REMARKS. This material is part of the sample from CRB 42 from which Bristow & Parodiz (1982) also identified *A. sulcatus* (Conrad). These other specimens are discussed under *Hemisinus* sp. The present specimens are here assigned to *Aylacostoma*, because of the definite ramp and shoulder which are first developed at a much smaller shell size than in the living *A. glabrum* Spix. In the latter the spiral sculpture also tends to be rather variably developed. No comparable fossil species are known.

Subclass **PULMONATA** Cuvier, 1834
Order **BASOMMATOPHORA** Keferstein, 1864
Superfamily **LYMNAEACEA** Blainville, 1825
Family **FERRISSIIDAE** Walker, 1917

[Subfamily Ferrissiinae Walker, 1917: 2, *nom. transl.*?Zilch, 1959: 126]

Genus ? ***HEBETANCYLUS*** Pilsbry, *in* Baker 1914

TYPE SPECIES. *Ancylus moricandi* d'Orbigny, 1837: 355. Recent, Brazil.

REMARKS. The supraspecific arrangement of this group has not been fully investigated because of its unimportance in the faunas studied herein. Thiele (1931: 482–3) did not recognize Ferrissiinae Walker and regarded *Hebetancylus* as a section of *Protancylus (Burnupia)* within the Ancylidae. Zilch (1959: 105) placed *Protancylus* (Recent, Celebes) in the Planorbidae, whilst *Burnupia* (Ferrissiidae) has a living South African type species. Zilch's work is possibly the first in which Ferrissiinae are raised to family level. These simple, patelliform, shells exhibit few easily recognized distinguishing features, and Walker placed much reliance on radulae to distinguish between genera. Zilch arranged a number of subgenera, including South American *Hebetancylus*, in the living Tasmanian genus *Ancylastrum* Bourguignat. The present specimen is provisionally assigned to *Hebetancylus* on its similarity in shell shape to illustrations (Zilch, 1959: 127, fig. 418) of the much larger (length 10–12 mm) type species, *H. moricandi* (d'Orbigny). Type material of this species was catalogued (Gray, 1854: 26, species no. 242) as being absent from the

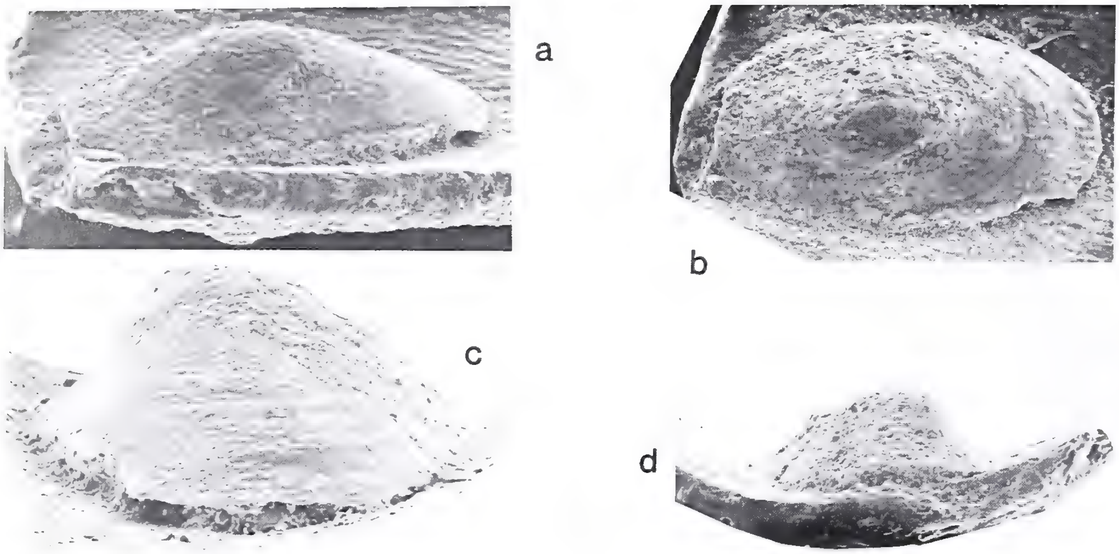


Fig. 294 *Hebetancylus* sp. Pebasian; Pichana, Peru; Hauxwell Colln. GG21570; specimen attached to fragment of bivalve shell. a, right hand side, × 50; b, apical view, × 50; c, front, × 100; d, rear, × 50.

d'Orbigny Collection in BMZD, and no authenticated specimens from other sources are available for comparison in BMZD.

Uncancylus (Pilsbry, 1914) (Recent, Brazil) is radially ribbed and has a pointed apex, whilst the Recent Peruvian *Anisancylus* (Pilsbry, 1924) is more tumid than *Hebetancylus* and its apex is situated near the left margin of the shell.

The present occurrence is thought to be the first definite fossil record of Ferrissiidae from South America. Parodiz (1969: 168) provisionally referred *Ancylus humboldti* Mayer Eymar (1900) from the ?Palaeocene of Chile to *?Palaeoancylus* of the Ancylidae. Willard's (1966: 66) record of the brachiopod *Lingula* in a Pebasian fauna from Negro Urca may possibly be based on a member of the Ferrissiidae, many of which can resemble *Lingula* in shape.

The Ferrissiidae live in fresh water. Pilsbry (1914) recorded *Gundlachia* living on dead leaves and other debris on the bottom of pools.

?Hebetancylus sp. Fig. 294

Material studied. BMPD GG21570, Late Caenozoic, Pebasian; Pichana, Peru. Obtained from washings, 1982, from residues of Hauxwell Colln, 1870. No other records.

Dimensions. l, 1.1 mm; br, 0.6 mm; h, 0.25 mm.

Description. The shell is elongate oval and over twice as long as broad. It is comparatively low, with both the anterior and posterior slopes lying at about 30° from the horizontal. The apex is possibly rather worn and is smoothly rounded. It is situated not far behind mid-shell length and is bent, not very strongly, to the left. Traces of growth lines are visible only on part of the anterior slope.

Remarks. The shell is not sufficiently well preserved to reveal any changes that may have occurred representing any postneanic metamorphosis. This, and its small size, make firm generic determination unwise. The shell adheres, presumably as in life, to a broken fragment of a bivalve, probably *Mytilopsis*.

Order **STYLOMMATOPHORA** Schmidt, 1855
Superfamily **ORTHALICACEA** Albers & von Martens, 1860

[Orthalicea (rank unknown) Albers & von Martens, 1860: 209, *nom. transl.* Burch, 1976: 132 as Orthalicoidea. = Superfamily Bulimulacea Fischer, 1883: 474, as Bulimulidae, *nom. transl.* Thiele, 1931: 651]

Although both Thiele (1931) and Zilch (1960) use the name Bulimulacea for the superfamily, Orthalicacea clearly has priority, as has been recognized in recent years by a few authors (Baker 1956: 133; 1963: 226; Burch 1976: 132) whilst Parodiz (1969: 179) used both names. The early works of Albers & von Martens (1860) and Tryon (1866*a*) were ignored by subsequent authors. In Fischer's (1883) classification, the Bulimulidae and Orthalicidae both had familial rank. Pilsbry (1899: 99; 1902: viii, x, lvii) produced his own classification, apparently in ignorance of Fischer's work, in which the Orthalicinae were placed as a subfamily of the Bulimulidae. This difference in rank of at least one grade has persisted in most later works of substance (Strebel 1909; Thiele 1931; Zilch 1960).

Family **ORTHALICIDAE** Albers & von Martens, 1860

[*nom. transl.* Tryon, 1866*a*: 223; also Fischer, 1883: 473; Taylor & Sohl, 1962: 12]

Genus ***ORTHALICUS*** Beck, 1837

[*Orthalicus* Beck, 1837: 59]

Type species. *Buccinum zebra* Müller, 1774: 138. By subsequent designation of Herrmannsen, 1847: 159, as *Bulimus zebra* Müller, Recent, probably South America. See Remarks, below.

Generic distribution. Recent; tropical South America, Central America, West Indies (Zilch 1960: 514). Southern

Florida, near sea, inferred to be introduced (Pilsbry 1946: 31). Fossil, first record herein: Late Caenozoic, Upper Amazon Basin. [*Orthalicus* is a tree snail.]

Diagnosis. Orthalicidae with a regular bucciniform shell shape; spire angle constant throughout growth, except for a rather obtuse apex; columella, simple, not strongly twisted; shell with microsculpture of spirally and collabrally arranged rows of pits.

Remarks. No attempt has been made to resolve the designation or identity of the type species of *Orthalicus*. Hermannssen's (1847) designation was of *Bulimus*, not *Buccinum*, *zebra* Müller. Pilsbry (1899: 104) argued that Müller's original description was too vague to be recognizable, though Rehder (1945) suggested that *B. zebra* was probably conspecific with *Orthalicus maracaibensis* Pfeiffer (1856) and *Bulimus undatus* Bruguière (1789). This last-named species was chosen by Zilch (1960: fig. 1795) to illustrate the genus *Orthalicus*.

Parodiz (1969: 179–184) recorded six fossil 'Bulimulacea', including one member of the Orthalicinae, from the Eocene onwards in South America. None resemble the present species, which he did not mention.

Orthalicus linteus (Conrad, 1871) Fig. 295

*v 1871*b* *Bulimus linteus* Conrad: 195; pl. 10, fig. 9.
. 1878 *Bulimus linteus* Conrad; Boettger: 149.

Holotype. NYSM 9157, Late Caenozoic, Pichana (Hauxwell Colln). No other material studied.

Further distribution. Pebas, two young shells (Boettger, 1878).

Diagnosis. *Orthalicus* with very regularly arranged microsculpture of close-set shallow pits; growth lines not bunched into rugae; spire angle about 50°; columella simple, untwisted, not plicate.

Description. The specimen is damaged, the apex eroded and the last half whorl largely decorticated; about six whorls are present. Although the lower part of the aperture is missing, the internal mould virtually corresponds with the true height of the shell. During fossilization, the external shell of the last and penultimate whorls have been forced apart. Where undamaged, the suture is simple and abutting, and not carinate as Conrad described. The whorl is gently convex in profile and is widest at the abapical suture. With the exception of the apex, which is more obtuse, the spire angle remains constant at about 50° throughout growth. The aperture had been carefully cleaned, presumably by Conrad, but there is no sign of a columellar plication. Traces of thin callus remain on the inner lip. The microsculpture consists of minute shallow pits arranged both spirally and along the prosocline growth lines.

Dimensions. h,40.5 mm; br,25.7 mm; hap,20.8 mm; sa *c.* 50°

Remarks. Conrad (1871*b*) pointed out that this was the only land snail in Hauxwell's collection from Pichana. The infilling of matrix typical of Pichana shows that it is definitely a fossil specimen. Living species of *Orthalicus* that I have examined possess a similar type of microsculpture but, in all cases, it is both much coarser and more irregular than in *O. linteus*. In addition, their growth lines are frequently bunched into rugae. Many living species illustrated by Tryon (1899) and Strebel (1913) appear to have a shell shape very similar to that of *O. linteus*, but it is felt that these comparisons are not exhaustive enough to show conclusively that *O. linteus* is extinct. Although it is certainly very unlikely to be of any great geological age, it is definitely a fossil specimen.

Conrad (1871*b*), whose work preceded the classifications of both Fischer (1883–7) and Pilsbry (1899–1902), assigned his species to *Bulimus*. As mentioned above, his description referred to the last whorl being slightly carinated at the suture. This, however, is because of damage to the shell, and is of no taxonomic significance; the suture would have been abutting in the original state as with the earlier whorls.

Conrad suggested that his species had some affinity with *Plectostylus* Beck, but the latter is pupiform with a relatively large body whorl and small aperture. Its spire angle reduces from about 90° to under 50° by the final whorl. Moreover, in *Plectostylus* the widest point of its whorls lies well above the suture (Zilch 1960: 483, fig. 1699). The simpler and more regularly geometrical growth and resulting shape of Conrad's fossil species is strongly reminiscent of Orthalicidae, and, in

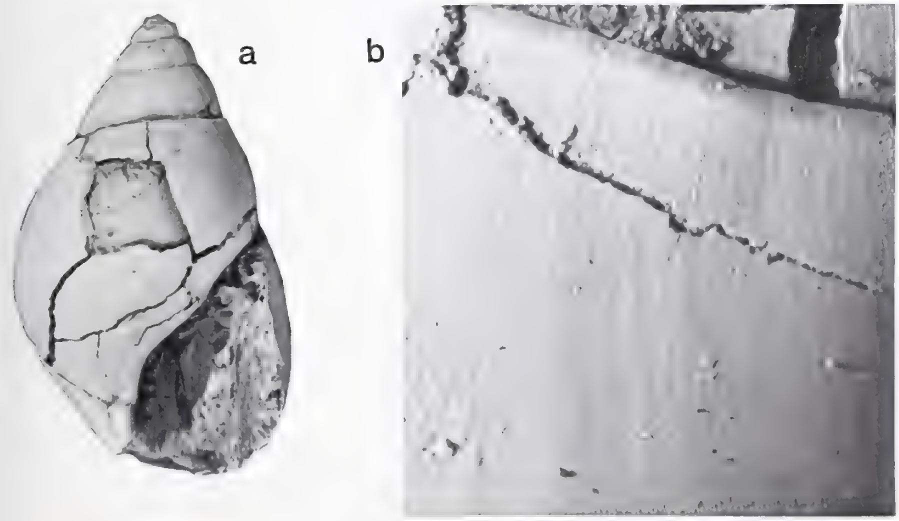


Fig. 295 *Orthalicus linteus* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. NYSM 9157; holotype of *Bulimus linteus* Conrad, figured by Conrad (1871: pl. 10. fig. 9). a, front, × 1.5; b, microsculpture of upper sutural region of right hand side of body whorl, × 10.

particular, of *Orthalicus* itself. Features in common include a similar type of microsculpture and apertural features, as well as a rather simple, untwisted columella lacking a plication. *B. linteus* Conrad is therfore assigned to *Orthalicus* with confidence, even though distinctions between genera are so dependent on anatomical features.

Class **BIVALVIA** Linné
Subclass **PALAEOHETERODONTA** Newell
Order **UNIONOIDA** Stoliczka (= NAIADES, auctt.)

Parodiz & Bonetto (1963) separated the Mutelacea as a distinct superfamily from the Unionacea; the Mutelacea comprising the African family Mutelidae Gray, 1847 and the South American Mycetopodidae Gray, 1840, both of which have lasidium larvae as opposed to the better known glochidia of the Unionacea. In addition, the present preliminary survey, confined to South American naiades, suggests that the two superfamilies may have a significant difference in their shell structure. All Mycetopodidae examined have markedly thicker prismatic layers than do the Hyriidae (Unionacea).

The classification of Parodiz & Bonetto is followed here, in preference to that used by Haas (1969*a*; *in* Moore 1969*b*). Haas also gave contradictory views on the authorship of suprageneric taxa in these two works, whereas, after careful checking, Parodiz & Bonetto (1963) have proved to be substantially correct.

The original distinction between lasidium and glochidium larvae was noted by von Ihering (1893), whose work Simpson (1900: 502) regarded as the then most important discovery in the study of the naiades. The acceptance of the implications of Ihering's observation seems to have been delayed, largely owing to the lack of confirmation by other workers. Ortmann (1911: 129–130) distinguished between Hyriinae with glochidia and Mutelinae with lasidia, but placed both in the same family Mutelidae. He persisted in giving the same classification (1921), even though he illustrated (1921: 469, text-fig. 4) the glochidia of twelve species of Hyriinae (mainly *Diplodon*) but omitted any information on the lasidia of Mutelinae dealt with in this later work. Marshall (1931*a*: 18–19) pointed out that von Ihering was the only worker to have seen lasidia and seemed to dismiss his observations as unfounded. Cox (*in* Moore 1969: N96), however, briefly noted the existence of three types of 'Unionacean' larvae: the **glochidium**, the **haustorial** larva of the African *Mutela bourguignati* (Ancey), and thirdly the **lasidium** of some South American species, whose developmental history still had to be studied in detail. Cox was apparently unaware of the work of Parodiz & Bonetto (1963), whilst his reference to the development of *Mutela bourguignati* was presumably based on the work of Fryer (1961), though it was not referred to in any of the Bivalve *Treatise* bibliographies. Parodiz & Bonetto had, however, discussed Fryer's results at some length. They had concluded that although there were differences between haustorial and lasidium larvae, their basic structure was broadly similar and that the inclusion of both in the Mutelacea was justifiable, whilst both were clearly very different from the glochidium of Unionacea.

The correct classification of Woodward's (1871) '*Anodon*' *batesi* from Pichana, p. 275, presented a problem. It has a shell outline reminiscent of some smooth-shelled *Diplodon* (Hyriidae), *Anodontites* (Mycetopodidae) and even the Central American *Brachyanodon* Crosse & Fischer, 1893 (Unionidae, Anodontinae). Taylor, Kennedy & Hall (1969), when working on bivalve shell structure, were unaware of the superfamilial separation of the Mutelacea by Parodiz & Bonetto (1963) (J. D. Taylor, personal communication). By chance, with the exception of two members of the Etheriidae, all the other naiades whose shell structure they had examined were Unionacea (*sensu* Parodiz & Bonetto): none were Mutelacea. I have therefore examined, without sectioning, several species of both *Diplodon* and *Anodontites*. In *Diplodon* the outer prismatic layer is too thin to be seen clearly. The shell structure of *Triplodon* (Hyriidae) is similar. In contrast, in *Anodontites* the prismatic layer is noticeably thicker and the honeycomb patterning of the shell surface below the periostracum is also clearly visible under low magnifications: '*A.*' *batesi* Woodward is here placed with confidence in *Anodontites* because it shows this shell structure. Other South American Mutelacea showing this coarse, easily visible, prismatic layer are *Mycetopoda*, *Fossula* and *Monocondylaea*. It thus appears that such differences in shell structure may well be a feature separating the two superfamilies, but such a proposition needs more thorough testing. This feature has been noted before: Marshall (1931*a*: 19) wrote that in some South American Mutelidae the prismatic layer was very thick.

Marshall's main line of research was concerned with the sculpturing of the periostracum, which may also be a diagnostic character at superfamilial level. Initially, he noted (1925: 1) the absence in *Diplodon* and other 'Unionidae' of microscopic radiating threads which were present in South American 'Mutelidae' (=Mycetopodidae). Expanding this study to a world-wide basis, he concluded that these striae occured in virtually all 'Mutelidae' (=Mutelacea) with the possible exception of *Mycetopoda* (1925: 12).

Taxonomy of naiades at both generic and specific level is complicated by the vast number of nominal species which have been erected. G. B. Sowerby illustrated nearly seven hundred species in his rather uncritical monographs of *Unio* (1864–68) and *Anodon* (1867–70). Later, Simpson (1900: 505–7) still recognized as valid over one thousand species in his catalogue, in spite of efforts to eliminate unnecessary taxa in synonymy. Of the 101 species of living Unionacea (all Hyriinae) from South America, he assigned 73 to *Diplodon*, s.l., whilst some 80 species of Mutelacea were from that continent. Considerably fewer species were recognized as distinct by Haas (1969*a*), but many of his synonymies and hence details of distribution remain suspect. The lack of comparative material on which to base taxonomic decisions is highlighted by the fact that the BMZD general (i.e. other than type and figured) material of South American naiades amounts to only seven drawers containing under 500 shells. Study of fossil forms is often further hampered by, among other things, the lack of knowledge of the hinge in a group in which there is often remarkable similarities of the external shell in unrelated toothed and edentulous genera.

In view of the relatively few South American fossil species known (26 in Parodiz, 1969) and the difficulties of establishing their relationships with each other and with living taxa, the naiades are of little stratigraphical value except in purely local contexts. An example of such use is the distribution of *Diplodon longulus* (Conrad), p. 270, which provides some confirmation that Singewald's (1928) locality at Paucarpata is Pebasian.

Naiades, probably because of their exclusively fresh-water distribution, are uncommon in the Pebasian. The holotype of *Anodontites batesi* (Woodward, 1871) is the only specimen

Table 1 List of Naiades from Pebasian and related localities. For full list of Cuenca Basin fossils see both Bristow & Parodiz (1982) and herein, pp. 339–41.

A, dealt with in further detail below. B, dealt with by Parodiz (1969). C, material thought to be lost as it is neither listed in Richards (1968, ANSP), nor Clarke (1906, NYSM), nor present in BMPD.

	Bivalve allied to *Mulleria* Conrad, 1871*b*: 192; Pichana. In NYSM; see Clarke, 1906. Presence noted in introduction to paper, fossil not described.
A	*Anodon batesi* Woodward, 1871: 103; pl. 5, fig. 10; Pichana. See p. 275.
C	*Anodonta pebasana* Conrad, 1874*a*: 29; pl. 1, fig. 5; ? Pebas.
ABC	*Triquetra longula* Conrad, 1874*a*: 29; pl. 1, fig. 10; ? Pebas. See p. 270.
ABC	*Triquetra longula* ('young') Conrad, 1874*a*: 30; pl. 1, fig. 13; ? Pebas. see p. *271*.
C	*Haplothaerus capax* Conrad, 1874*b*: 83; pl. 12, figs 1, 2, 3; Iquitos.
	Unio sp.; Boettger, 1878: 498; Pebas (fragment).
C	*Anodon* sp.; Etheridge, 1879: 84; cliffs near Canamá, shell fragments only.
C	*Unio* sp.; Etheridge, 1879: 84; as above.
	Anodonta sp.; Roxo, 1924: 45; Três Unidos, Peru, fragments.
	Unio sp.; Roxo, 1924: 45; Cachoera das Tracoas, Brazil, abundant shells, not identified because of lack of comparative material and literature.
	Hyria corrugata (Lamarck); Roxo, 1924: 45; Três Unidos, Peru [= *Prisodon*].
	Castalia ambigua (Lamarck); Roxo, 1924: 45; locality not given.
AB	*Prodiplodon singewaldi* Marshall, 1928*a*: 2; pl. 1, figs 3, 6; Paucarpata, Marañon River. See *Diplodon longulus*, p. 270.
B	*Prodiplodon bassleri* Marshall, 1928*a*: 3; pl. 1., fig. 1; Pebas.
AB	*Prodiplodon paucarpatensis* Marshall, 1928*a*: 4; pl. 1, fig. 4; Paucarpata, Marañon River. See *Diplodon longulus*, p. 270.
AB	*Eodiplodon gardnerae* Marshall, 1928*a*: 4; pl. 1, figs 2, 8; Pebas. Placed in *Diplodon* by Parodiz (1969: 70; pl. 3, figs 2, 4); see p. 267.
AB	*Eodiplodon pebasensis* Marshall, 1928*a*: 5; pl. 1, figs 5, 7; Pebas. Placed in synonymy of *D. gardnerae* by Parodiz (1969: 70; pl. 3, figs 1, 3 which are copies of Marshall's type illustrations); see p. 267.
	Anodontites ?; Marshall, 1928*a*; 6; Taropoto, Peru, fragments only.
	Castalioides laddi Marshall, 1934: 78, figs 1–3; 'Pleistocene', Venezuela.
	'Nayad' shell fragment; de Greve, 1938: 19, text-fig. 1; Iquitos (See Willard, 1966, below).
A	*Hyria* sp.; de Greve, 1938: 20; pl. 7, figs 24, 25; Iquitos. See *Diplodon longulus*, p. 270.
	Hyria trinitaria Maury 1925*b*; Palmer, 1945: 12; pl. 1, figs 1–10; Late Caenozoic, Venezuela.
	Hyria weisbordi Palmer, 1945: 13; pl. 3, figs 11, 12; as above.
	Prodiplodon tipswordi Palmer, 1945: 16; pl. 3, figs 4, 9–12; as above [= *Diplodon*].
	Castalioides laddi Marshall; Palmer, 1945: 17; pl. 2, figs 17–22; 'Plio-Pleistocene', Venezuela.
A	*Trilodon* (*sic*) et *Triplodon latouri* Pilsbry (*sic*, for *Triplodon latouri* Pilsbry & Olsson, 1935); Willard, 1966: 66, 67, 90; pl. 56, fig. 1; Negro Urca on Rio Negro 200 km NW of Iquitos (figured specimen) and Barranco, above Rumi Tuni 225 km N of Iquitos on Rio Napo. Misidentified; see under *Diplodon longulus* (Conrad), p. 270.
	Anodontites lacivensis (*sic*) Pilsbry & Olsson (for *Anodontites laciranus* Pilsbry & Olsson); Willard 1966: 90; pl. 56, fig. 2; Iquitos. Misidentified; probably same as 'Nayad-shell' of de Greve, 1938, above.
A	*Diplodon (Ecuadorea)* sp. aff. *bristowi* Parodiz *in* Bristow & Parodiz, 1982; herein; La Tagua, Loc. 54. See p. 273.

known from Pichana. The Naiades are represented only by shell fragments of large specimens of Mutelacea from both Puerto Nariño and Weeda's La Tagua locality (p. 172). A single valve referred herein to *Diplodon* (*Ecuadorea*) sp. aff. *bristowi* Parodiz (p. 273) was found at La Tagua, Loc. 54. With the exception of Roxo's (1924) reference to abundant shells of *Unio*, all the records below are of few, often single shells. In contrast, naiades are a more important element in both the Cuenca Basin (Liddle & Palmer 1941, Bristow & Parodiz 1982) and Venezuelan Pliocene faunas described by Palmer (1945). Four species, all assigned to different genera, were described by Pilsbry & Olsson (1935) from the La Cira Formation fauna, which totalled fourteen molluscan species in all.

Parodiz (1969) reviewed some of the Pebasian species. His comments on both generic and specific synonymies are extremely useful. Unfortunately his records are far from complete and his re-illustrations of type specimens are accompanied by sometimes ambiguous plate explanations. A new list, Table 1, of all Pebasian and other relevant species is therefore given in date order. No Pebasian species are known to occur in other deposits though two were identified as living species (Roxo, 1924).

Superfamily **UNIONACEA** Fleming, 1828

[*nom. transl*. Thiele, 1934: 815, *ex* Unionidae Fleming, 1828: 415].

Family **HYRIIDAE** Swainson, 1840

[*nom. transl*. Parodiz & Bonetto: 1963: 204, *ex* Hyrinae Swainson, 1840: 282 *et* Hyrianae Swainson, 1840: 379].

Subfamily **HYRIINAE** Swainson, 1840

[*nom. conserv*. under Article 40 of I.C.Z.N. (1961); see Haas *in* Moore, 1969*b*: N457].

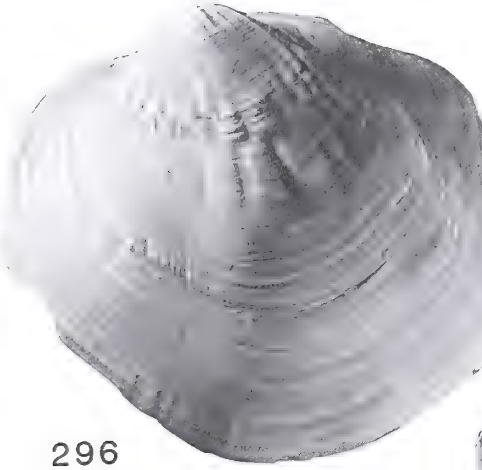
Parodiz & Bonetto (1963) appear to be the first authors to use the family name Hyriidae. Presumably their quotation of Hyriadae 'Agassiz, 1847' can refer only to his *Nomenclatoris zoologici*, the molluscan part of which appeared in 1845. In it (1845: 43), Hyrianae is listed but there is no reference to Hyriidae. Both editions of the accompanying *Index universalis* (1846, 1848) gave the same usage.

The Hyriinae are the only members of the Unionacea found in South America both during the Caenozoic and at the present day (Parodiz & Bonetto 1963: 196; map 3). Other subfamilies of the Hyriidae live in Australia.

Genus ***DIPLODON*** Spix, 1827

TYPE SPECIES. *Diplodon ellypticum* Spix, *in* Spix & Wagner 1827, by subsequent designation of Simpson (1900: 872). Recent, Santo Francisco River, eastern Brazil.

DIAGNOSIS. Moderately-sized Hyriinae, moderate- to thin-shelled; outline variable, elliptical to suborbicular, non-alate or only weakly so; hinge line slightly curved; sculpture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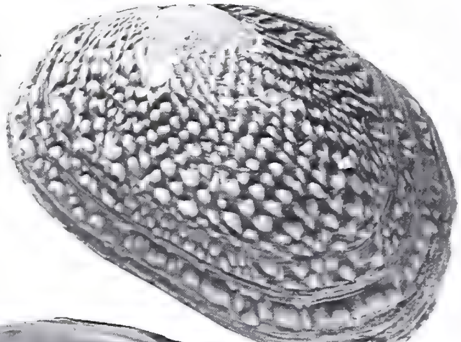
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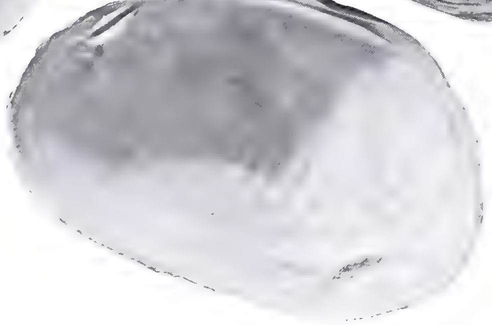

297b

Fig. 296 *Rhipidodonta paranense* (Lea). Recent; Corrientes Prov., Argentina; d'Orbigny Colln. BMZD 1854.9.4.41; left valve, × 1.5.
Fig. 297 *Iridea granosa* (Bruguière). Recent; French Guiana. BMZD 1901.12.14.15; a, left valve exterior; b, right valve interior; both × 2.

basically of chevron pattern of ribs or tubercles, often confined to umbonal region, but sometimes spreading to ventral commissure; anterior and posterior regions of shell usually smooth except for moderately rugose growth lines. One or two anterior cardinals in left valve, two in right valve; dorsal cardinal tooth lamelliform; main, more ventrally situated cardinal granulose or striate, frequently bicuspid or even split into two separate teeth (see Remarks); posterior lamellar teeth elongate, two in left valve, one in right. Glochidia, parasitic or non-parasitic.

SPECIES ASSIGNED. Seventeen Tertiary fossil species (Parodiz 1969) and *Triquetra longula* Conrad (1874*a*), Pebas. For living species see Simpson (1900, 1914), who listed over 70 species, and Haas (1969*a*) who recognized 22 full species.

DISTRIBUTION. Palaeocene to Recent, South America (Simpson 1900, Parodiz 1969).

REMARKS. Parodiz (1969: 49), with further alterations in Bristow & Parodiz (1982: 22) synonymized several taxa which are given generic or subgeneric status by Haas (*in* Moore 1969*b*: N458–461). The arrangement followed here is given below and follows fairly closely that of Bristow & Parodiz (1982):

(1) *Diplodon*, s.s. [= *Diplodon*, *Iridea*, *Prodiplodon*, *Eodiplodon*, *Schleschiella*]. Shells usually longer than high; glochidia parasitic.
(2) *Diplodon (Ecuadorea)* [= *Ecuadorea*, *Castalioides*]. Shells usually longer than high; umbonal sculpture strongly developed, sometimes spreading to ventral commissure; glochidia non-parasitic.
(3) *Diplodon (Rhipidodonta)* [= *Rhipidodonta*, *Cyclomya*, *Bulloideus*]. Shells suborbicular; glochidia non-parasitic.

This scheme must be regarded as no more than a compromise. To a certain extent, shell shape and sculpture intergrade between the three subgenera, and in addition the glochidia of many species are unknown. *Bulloideus* Simpson (1900: 887), type species *Unio bulloides* Lea (1859), is here placed in *Rhipidodonta* Mörch (1853) whose type species is the rather similar (Fig. 296) *Unio paranensis* Lea (1834). Some confusion may have arisen because the illustration given by Haas (*in* Moore 1969*b*: fig. D51/2a–c) is of a completely different species, being based on a misidentified figure from Küster (1861: *Anodonta* pl. 85, fig. 3). None of the fossils dealt with below are referable to *Rhipidodonta*. All the other *Treatise* illustrations of the taxa referred to above are correctly identified with the important exception of *Diplodon* itself: See p. 269.

Parodiz (1969) has first included *Antediplodon* Marshall (1929), from the Pliocene of Texas, in the synonymy of *Diplodon* but omitted it later (Bristow & Parodiz 1982: 22), probably a sound decision. The characters of *Antediplodon* are unclear from the original illustration (copied by Haas, *in* Moore 1969*b*: fig. D50/1). Its inclusion in *Diplodon* would represent the only occurrence of the genus outside South America, for it appears to be completely absent from Central America as well as northernmost South America (Parodiz 1969: 50; map 2). Other changes by Bristow & Parodiz (1982) include the formal recognition of *Ecuadorea* as a subgenus distinct from *Rhipidodonta*. Previously, Parodiz (1969) had formally described all the species with which he had dealt as members of *Diplodon*, though (1969: 51) he had given a key distinguishing between *Rhipidodonta* and *Diplodon* and had placed both *Ecuadorea* and *Schleschiella* in the synonymy of *Rhipidodonta*.

In *Diplodon* there are terminological problems in describing the cardinal teeth. There is a lamelliform dorsal anterior tooth in the right valve, whilst a similar tooth occurs rarely in the left valve (as in the larger syntype of *D. ellypticus* but not in other specimens referable to that species). The main cardinal tooth below is irregular in form and frequently bicuspid. In some cases the cusps are separated by such a deep cavity that they may be described as two separate teeth: different authors' descriptions become difficult to reconcile in such circumstances. Examination of the main cardinal tooth of several species assigned to *Diplodon* (s.l.) suggests that differences are not necessarily specifically diagnostic and are therefore almost certainly not of generic importance.

Subgenus ***DIPLODON*** Spix, 1827

[= *Iridea* Swainson, 1840; type species *Unio granosus* Bruguière 1792*b*, by monotypy; Recent, French Guiana. *Prodiplodon* Marshall, 1928*a*; type species *P. singewaldi* Marshall 1928*a*; by original designation; Neogene (?Pebasian), Paucarpata, Peru. *Eodiplodon* Marshall, 1928*a*; type species *E. gardnerae* Marshall 1928*a*, Neogene, Pebas Formation, Peru. *Schleschiella* Modell, 1950; type species *Unio burroughianus* Lea 1834, by original designation. Recent, Brazil].

TYPE SPECIES. See p. 265, under genus.

DIAGNOSIS. Hyriinae with oval outline; normally non-alate; posterior angulation weak, if present; sculpture usually confined to umbonal region; glochidia parasitic (when known).

SPECIES ASSIGNED. Fossil. *Triquetra longula* Conrad 1874*a*, Pebas; *Prodiplodon bassleri* Marshall 1928*a*, Pebas; *Eodiplodon gardnerae* Marshall 1928*a*, Pebas. *Prodiplodon tipswordi* Palmer 1945, ?Pliocene or Pleistocene, Venezuela.

Living. Sixteen full species and eight subspecies (Haas 1969*a*: 511–526.

DISTRIBUTION, Palaeocene to Recent, South America only (Parodiz 1969).

REMARKS. The genus is discussed at length by Parodiz (1969) and Bristow & Parodiz (1982: 22–25). In both these works and in Haas (*in* Moore 1969*b*) *Iridea* Swainson is placed in the synonymy of *Diplodon*. Its type species (Fig. 297) *Unio granosus* Bruguière is sculptured with tubercles arranged in a divaricate pattern and covering the whole shell surface. In spite of this obvious difference, the synonymy is probably sound. *D. granosus* and *D. ellypticus* are so similar in outline, convexity and hinge characters that some authors (e.g. Haas, 1969*a*: 525) have regarded the two as no more than distinct subspecies of *D. granosus*. It appears that the first valid type designation is that of Simpson (1900), quoted on p. 265, and repeated in his later work (1914: 1225). Haas (*in* Moore 1969*b*: N460) gave '*D. ellypticum*' as type species by original designation. This cannot be correct as four species were illustrated by Spix (1827) under *Diplodon*, with no indication as to which was the type. The name *Diplodon* was not used in the main unionid monographs (Küster 1861 (*Unio* & *Hyria*): 238; Sowerby 1868 (*Unio*): pl. 74, fig. 382). However, it was mentioned by Chenu (1862: 142), who gave none of Spix' species as examples, by H. & A. Adams (1857: 497), who gave '*D. ellypticum*' as one of twenty examples, and also by Fischer (1886: 1000) who gave '*D. ellipticum*' as his example (as opposed to type) of the genus, which (1886: 1004) he placed in the synonymy of *Hyria*.

A further problem common to several of Spix' names (including *Aylacostoma*, also dealt with here, p. 258) arises because of name changes by various of his co-authors, including Wagner. Spix was responsible for the plates, but he died in 1826, before publication of the joint work (1827). In the text (1827: 33) by Wagner, the species is described as '*Unio ellipticus*' Wagner with '*Diplodon ellipticus*' Spix placed in synonymy. As far as is known, both text and illustrations are part of a single work and were published simultaneously. On the advice of R. V. Melville, one-time Secretary of ICZN, I now propose that *Diplodon ellypticum* Spix 1827 is treated as having priority over *Unio ellipticus* Wagner 1827. There would seem to be some natural justice in this decision. Both the sequence of events and the fact that Wagner placed Spix' name in synonymy strongly suggests that Wagner changed Spix' name rather than *vice versa*. This decision also avoids the problem created by the fact that Wagner's name is a junior homonym of both *Unio ellipticum* Rafinesque 1820, and *U. ellipticum* Barnes 1823. This homonymy led Simpson (1900: 877) to propose *Diplodon wagnerianum* as a new name for *U. ellipticus* Wagner, *non* Barnes.

Thus, the generally accepted combination *Diplodon ellypticum* Spix, 1827, remains available for the type species of *Diplodon*, with Spix' original spelling corrected for the masculine gender. Both *Unio ellipticus* Wagner (1827) and *Diplodon wagnerianum* Simpson (1900) fall into its synonymy.

Diplodon (Diplodon) ellypticus Spix, 1827 Figs 298–300

*v 1827 *Diplodon ellypticum* Spix, *in* Spix & Wagner: pl. 26, figs 1, 2.

v 1827 *Unio ellipticus* Wagner, *in* Spix & Wagner: 33.

v. 1843 *Unio multistriatus* Lea; Hanley: 176; pl. 20, fig. 35.

non 1861 *Unio ellipticus* (Spix); Küster: 238; pl. 80, fig. 2 [= *Diplodon multistriatus* (Lea)]

v. 1868 *Unio ellipticus* (Spix); Sowerby: pl. 74, fig. 382.

. 1890 *Unio ellipticus* (Spix); von Ihering: 163; pl. 9, figs 8, 9.

. 1893 *Unio ellipticus* (Spix); von Ihering: 108, 114, 115.

*. 1900 *Diplodon wagnerianum* Simpson: 877.

. 1914 *Diplodon wagnerianum* Simpson: 1251.

? 1969*a* *Diplodon (Diplodon) granosus ellypticus* Spix; Haas: 525.

v. 1971 *Unio ellipticus* (Spix); Johnson: 103.

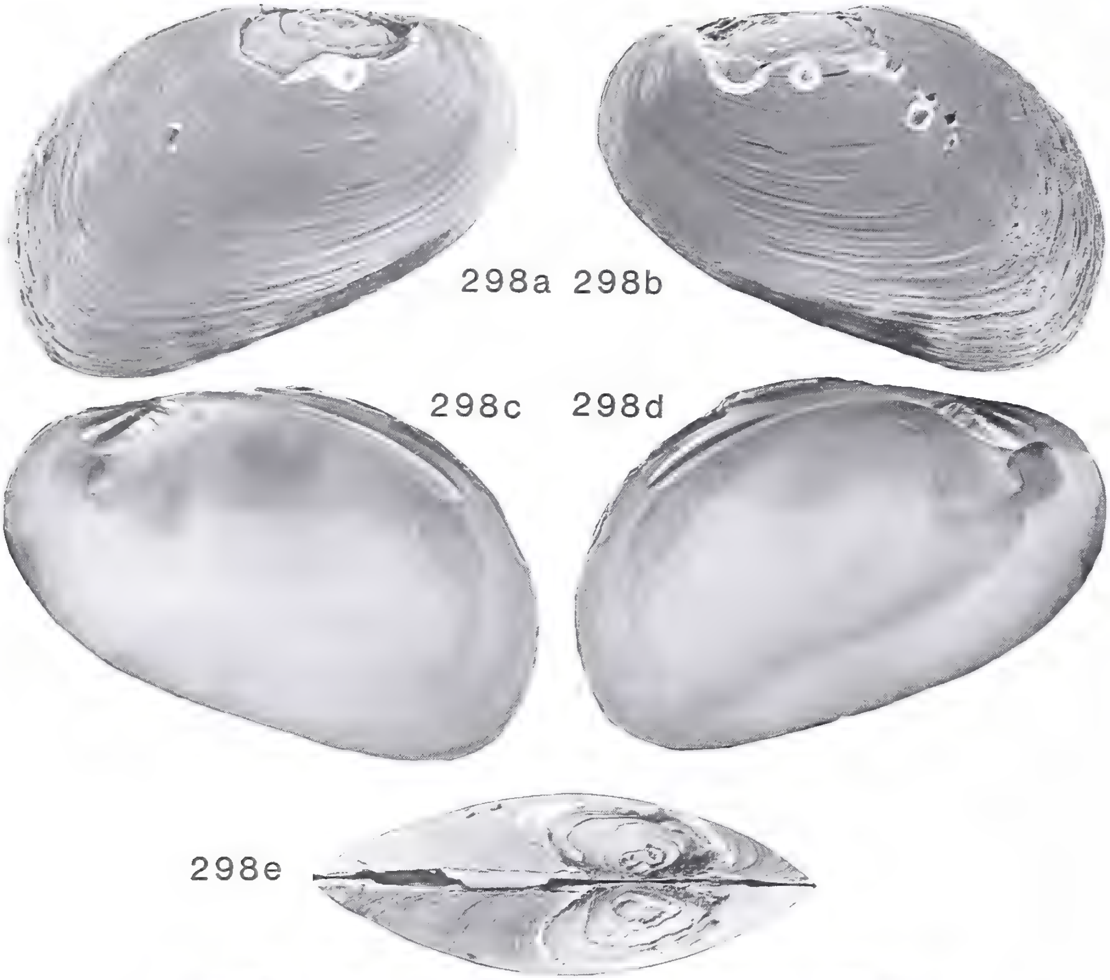
v. 1983*b* *Diplodon ellypticum* Spix; Fechter: 243; pl. F, figs 5, 6 (shells); pl. L, figs 1, 2 (labels).

SYNTYPES. Two specimens, neither of which was figured by Spix but both figured by Fechter (1983*b*); Recent, Rio Santo Francisco, eastern Brazil (Spix colln), Zool. Staatssammlung, München. A lectotype is not selected: see p. 269.

OTHER MATERIAL STUDIED. BMZD 1907.10.28.198, shell figured both by Hanley (1843) and by Sowerby (1868) and listed by Johnson (1971); labelled Bahia, Brazil (Hanley Colln); BMZD, two shells, Rio Concejo, Brazil (colln unknown). Also occurs in Rio Piracicaba and Rio Tamanduatahy, S. Paulo, Brazil (Ihering 1893). Recent only, eastern Brazil.

DIAGNOSIS. *Diplodon* with regularly oval outline narrowing towards anterior; greatest height at junction of ventral and posterior margins; sculpture of light irregular ribs, confined to small area around umbones.

DESCRIPTION. The umbones of all the few specimens available for study are eroded and the sculpture can be seen fairly clearly only on the specimen figured by Sowerby (1868). It consists of about 17 rather wrinkled ribs all lying anterior to the posterior area. They are approximately the same width as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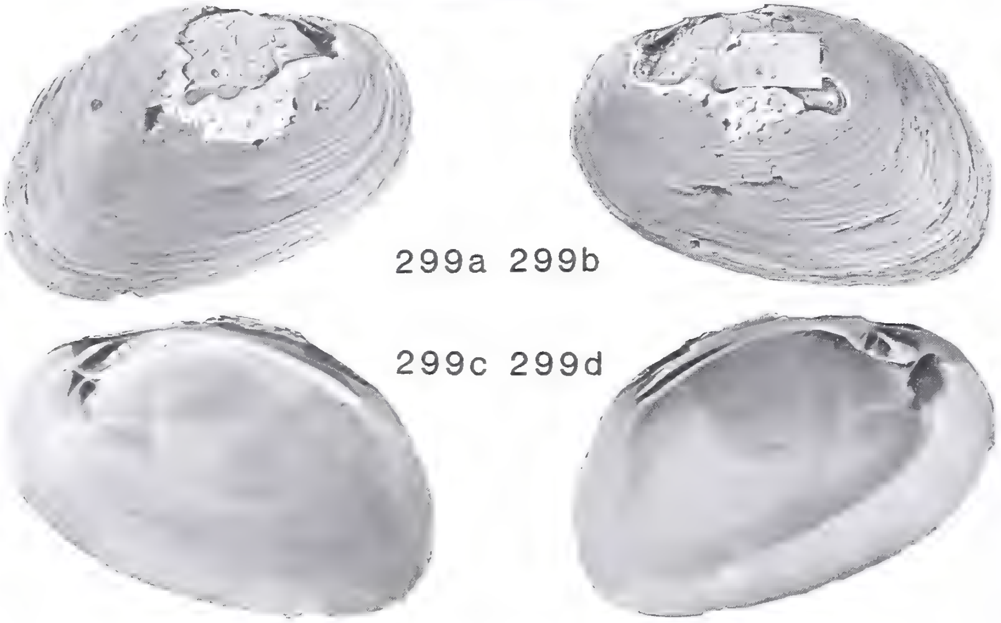
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Figs 298–299 *Diplodon ellypticus* Spix. Syntypes unfigured by Spix; Recent; Rio Saõ Francisco, Minas Gerais Province, Brazil; Spix Colln, Zool. Staatssammlung, München. **298**, specimen figured by Fechter (1983: pl. F, figs 5, 6) but not by Spix; a–e, ×1.5. **299**, a–d, × 1.5.

the major growth increments (*c*. 0.3 mm) and die out within 5–7 mm of the umbones. They are not radiating but lie subparallel to each other, more or less in a dorsoventral direction. The posterior area is smooth except for two or three randomly positioned, impersistent riblets which do not originate from the umbones. No specimens show traces of ribbing further than 10 mm from the umbones, and the remainder of the shell is smooth except for rather undulating growth increments of varying strength, and a tendency to become untidy and slightly scabrous near the valve margins. The shell is moderately thin. The beak cavities are shallow. In both dorsal and anterior view the shell is gently and simply convex, with no modification such as a posterior alation. The hinge is rather variable. In the right valve there are two cardinal teeth. The dorsal one is lamelliform, and runs forward from the umbo, diverging gently from the dorsal margin. Below it lies a much heavier cardinal tooth which is very striate, granular, and of irregular shape. It is frequently bicuspid, with the anterior cusp elongate and subparallel to the hinge whilst the posterior cusp is shorter and peg-like. There is normally one cardinal tooth in the left valve, very similar to the main cardinal of the right valve. In the largest syntype, however, there is a second, separate, cardinal tooth like the dorsal cardinal tooth present in normal right valves. There are two compressed, faintly crenulate, lamellar teeth in the left valve and one in the right. The crenulations are the surface expression of deep-seated differences in the structure of the semi-translucent nacreous shell. The ligamental nymphs appear to coincide in length with the posterior lamellar teeth, but their anterior ends are lost due to umbonal erosion. The anterior adductor scar is well marked, with the pedal protractor scar joined to its posteroventral margin. The posterior adductor scar is far less well marked, so that it is impossible to separate it from the posterior pedal retractor scar. The anterior pedal retractor scar is deep and situated below the anterior end of the cardinal teeth. The pedal elevator scarring consists of four or five irregularly positioned scars of varying shape and depth situated in the beak cavities: those of the left and right valves of the same individual do not form mirror images. The pallial line is entire and clearly visible.

DIMENSIONS. In mm.	l	h	br	l/h
Figd Spix (1827) and von Ihering (1890); specimen not seen, probably lost.	48	26	15	1.85
Unfig'd syntype (Zool. Staatssammlung, München).	49.3	31.0	16.9	1.59
Unfig'd syntype (as above).	38.8	25.0	14.1	1.55
BMZD 1907.10.28.198 (fig'd Hanley 1843; Sowerby 1868).	36.4	21.6	10.3	1.69
BMZD, Brazil	50.5	29.2	15.8	1.73
BMZD, Brazil	44.6	27.0	14.8	1.65

REMARKS. Von Ihering (1890) figured internal views of both valves of a shell from Spix' collection in Zool. Staatssammlung, München which closely resembles the type illustration (Spix 1827) in both shape and dimensions. This specimen cannot now be found, but two other shells in Spix' collection form the basis of the present description. Fechter (1983*b*: 243) wisely decided not to select either as lectotype. I also feel that lectotype selection is unjustified as there is always the possibility that the figured specimen will be found. It is a pity that von Ihering did not provide an external view. There seems little doubt, however, that he was dealing with Spix' figured specimen. In his description, he referred to the ribbing being confined to within 9–10 mm of the umbones.

Diplodon multistriatus (Lea) is quite similar to *D. ellypticus*, but may be distinguished by its coarser growth rugae, and its stronger sculpture, which persists for about 12 mm ventrally below the umbo and for up to 30 mm diagonally in a posteroventral direction. The anterior parts of both species are very similar in outline but in *D. multistriatus* the dorsal and ventral margins are more nearly parallel and the shell more elongate.

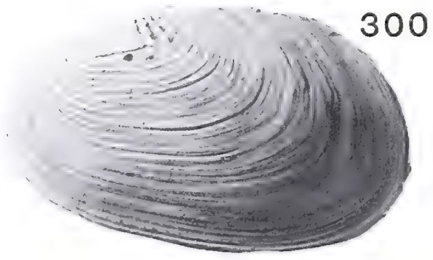
D. ellypticus and *D. multistriatus* have frequently been confused, and a synonymy of *Diplodon multistriatus* is given below to clarify the usage of various authors. Hanley (1843) figured as *Unio multistriatus* Lea the same shell that Sowerby (1868: pl. 74, fig. 382) later correctly identified as *ellypticus*. Sowerby (1868: fig. 455) also correctly identified *U. multistriatus*. He commented that it was now regarded by Lea himself as being identical with Spix' *ellypticum*, but 'if so, the shell . . . merits to be figured from its very remarkable sculpture.' Lea's opinion may have been made personally to Sowerby because I have been unable to find it published elsewhere. Both von Ihering (1890) and Simpson (1900; 1914) give extensive synonymies which are only partly correct.

Küster (1861) figured a specimen of *U. multistriatus* as *U. ellipticus*. His misidentification persists into the Bivalve *Treatise* where his figure is copied by Haas (*in* Moore 1969*b*: N459). In *Das Tierreich*, Haas regarded 1969*a*: 525–6) *D. ellypticum* and *D. multistriatus* as two distinct subspecies of *D. granosum* (Bruguière 1792*b*). His interpretation is suspect, the work being unillustrated. Moreover, he places *D. jacksoni* Marshall in the synonymy of *D. granosum ellypticum*, but Marshall's original illustration (1928*b*: pl. 4, fig. 1) shows a species in which the umbo is raised above the hinge and the ventral margin does not slope down towards the posterior.

Diplodon gratus (Lea 1860) from southern Brazil (BMZD) and the Uruguay River (Simpson 1900: 886) was assigned by Simpson to his new subgenus *Cyclomya* (= *Rhipidodonta* herein; see p. 266). However, its resemblance to *D. ellypticus* is such that the two ought to be compared. *D. gratus* may be distinguished by its greater size, less elongate outline and an incipient alation.

Diplodon (Diplodon) multistriatus (Lea, 1831) Fig. 301

* 1831 *Unio multistriatus* Lea: 91; pl. 12, fig. 22.
v. 1847 *Unio multistriatus* Lea; d'Orbigny: 607.
*. 1848 *Unio psammactinus* Bronn, *in* Philippi: 79; pl. 5, fig. 2.
*. 1848 *Unio granuliferus* Dunker: 182.
. 1856 *Unio psammactinus* Bronn; Küster (*Unio & Hyria*): 159; pl. 45, fig. 6.
. 1858 *Unio multistriatus* Lea; Chenu: pl. 11, fig. 2, 2a, b.
. 1860 *Unio granuliferus* Dunker; Pfeiffer: 150; pl. 39, figs 1–3.
. 1861 *Unio ellipticus* Wagner *in* Spix; Küster: 238; pl. 80, fig. 2 [*non* Spix].
v. 1868 *Unio multistriatus* Lea; Sowerby: pl. 85, fig. 455.
. 1890 *Unio multistriatus* Lea; von Ihering: 165 (*pars*).
. 1900 *Unio granosus* Bruguière; Simpson: 878 (*pars*).
? 1969*a* *Diplodon (Diplodon) granosus multistriatus* (Lea) Haas: 526.
. 1969*b* *Diplodon ellypticum* Spix; Haas, *in* Moore: N460; fig. D51/5a, b [*non* Spix].



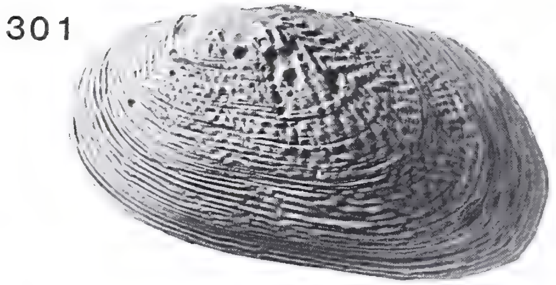


Fig. 300 *Diplodon ellypticus* Spix. Shell figured by Sowerby (1868: pl. 74, fig. 382) as *Unio ellypticus* and by Hanley (1843: pl. 20, fig. 35) as *Unio multistriatus* Lea. Recent; Bahia, Brazil, *ex* Hanley Colln. BMZD 1907.10.28.198; left valve, × 1.5.

Fig. 301 *Diplodon multistriatus* (Lea). Shell figured by Sowerby (1868: pl. 85, fig. 455) as *Unio multistriatus* Lea. Recent, Brazil; *ex* Hanley Colln. BMZD 1907.10.28.196; left valve, × 1.5.

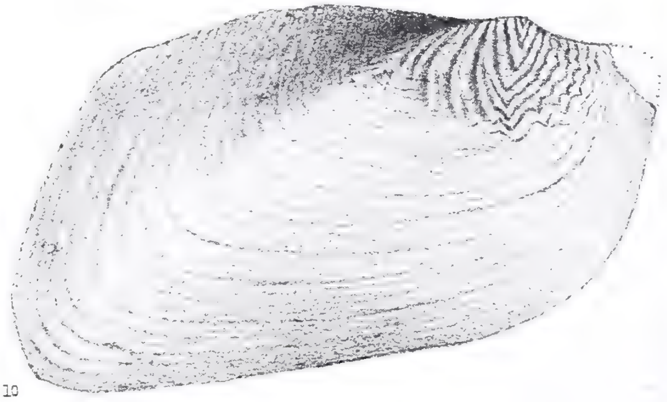


Fig. 302 *Diplodon longulus* (Conrad). Pebasian; ? Pebas, Old Pebas or Pichana, Peru; Steere Colln (presumed lost, ANSP); copy of type illustration; right valve.

HOLOTYPE. Probably lost. Lea stated that the shell he illustrated was in the collection of Mrs Mawe of London and its subsequent history is unknown. Johnson (1974*a*: 94), however, stated that USNM 84114 agrees with the illustration, but it was labelled as Moricand collection: it seems unlikely to be the holotype.

MATERIAL STUDIED. BMZD 1907.10.28.196. Shell figured by Sowerby (1868: pl. 85, fig. 455); BMZD 54.12.4.840, shell referred to by d'Orbigny (1847: 607). BMZD, 4 further specimens. Recent; occurs in coastal rivers of Brazil between Rio de Janeiro and Bahia (von Ihering 1890: 167, 1893: 115, 120); Rio Parahiva (d'Orbigny 1847).

DIMENSIONS. In mm.	l	h	br	l/h
BMZD 1907.10.28.196	43.5	23.2	12.1	1.88
BMZD 54.12.4.840	45.9	25.0	14.2	1.84

REMARKS. The above synonymy is not comprehensive. Several of the references given by both von Ihering (1890) and Simpson (1900) in their much fuller synonymies are clearly misidentifications. The shell figured by Sowerby (1868: pl. 74, fig. 382) as *U. ellipticus* (Spix) was wrongly included in *U. multistriatus* by von Ihering, who nevertheless was one of the few authors to notice that Küster's (1861) identification of *U. ellipticus* was incorrect. The type illustrations of *U. multistriatus* and *U. psammactinus* suggest that the two are conspecific, though von Ihering later changed his mind and separated the two (1893: 107). Simpson's (1900) reference of *U. multistriatus* to *U. granosus* implies an unacceptably large degree of variation within a single species.

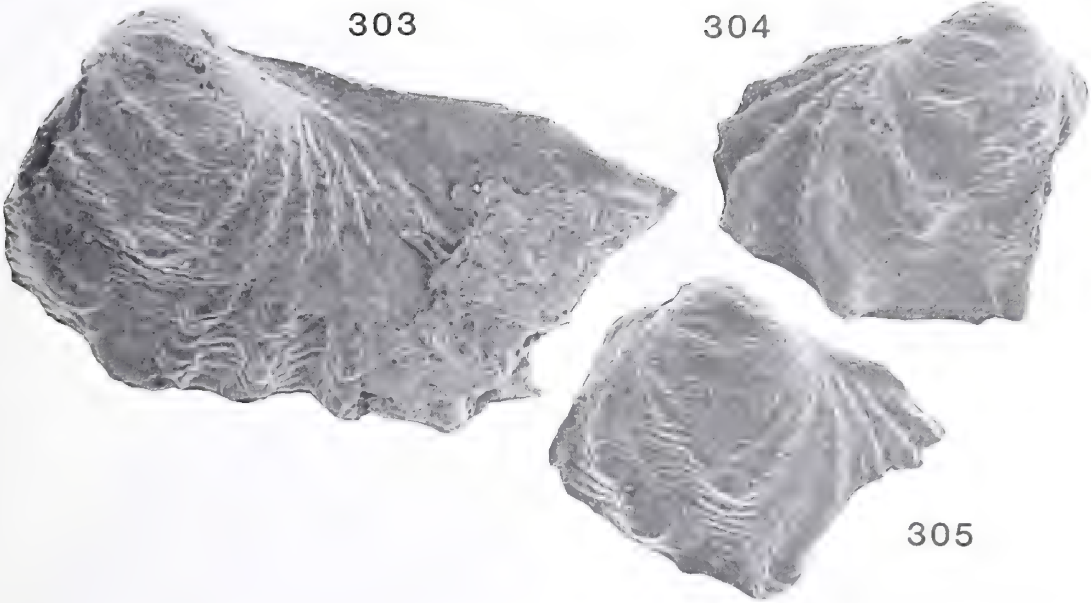
Diplodon (Diplodon) longulus (Conrad, 1874*a*) Fig. 302

* 1874*a* *Triquetra longula* Conrad: 29 (*pars*); pl. 1, fig. 10 (*non* 'young' [i.e. juvenile], p. 30; pl. 1, fig. 13).
. 1928*a* *Prodiplodon paucarpatensis* Marshall: 4; pl. 1, fig. 4.
. 1928*a* *Prodiplodon singewaldi* Marshall: 2; pl. 1, figs 3, 6.
. 1938 *Hyria* sp.; de Greve: 20; pl. 7, figs 24, 25.
. 1966 *Triplodon latouri* Pilsbry (*sic*, *pro* Pilsbry & Olsson, 1935); Willard: 90; pl. 56, fig. 1.
. 1969 *Diplodon singewaldi* (Marshall) Parodiz: 72; pl. 7, figs 1–3.
. 1969 ?*Triplodon longula* (Conrad) Parodiz: 77.

TYPE AND FIGURED SPECIMENS. Conrad's material is presumed lost, neither listed by Richards (1968) as being in ANSP, nor by Clarke (1906) as being in NYSM. Marshall's specimens are in USNM; de Greve's are in PIMUZ; Willard's, in Lehigh Univ., Bethlehem, Pennsylvania.

TYPE LOCALITY AND HORIZON (of *D. longulus*). Late Caenozoic, Pebasian; either Pebas, Old Pebas or Pichana, Peru.

FURTHER DISTRIBUTION. All presumed to be Pebasian. Paucarpata, on Marañón River, Peru (Singewald 1928, Marshall 1928*a*); Iquitos (de Greve 1938); Negro Urca, 200 km NW of Iquitos and Rumi Tuni in Napo River Valley some 225 km north of Iquitos (Willard 1966).



Figs 303–305 *Diplodon* sp. juv. Pebasian; Pichana, Peru; Hauxwell Colln. All × 50. **303**, LL28105; left valve. **304**, LL28106; right valve. **305**, LL28107; left valve.

Remarks. As the above synonymy is constructed entirely from published illustrations, no specimens having been examined, no attempt is made here to give a formal diagnosis and description of this species. It is characterized by its relatively quadrilateral shape, with the hinge line, posterodorsal and ventral margins all being comparatively straight. The v-shaped folding in the umbonal region is also well formed and clear. The rather similar *D. bassleri* (Marshall 1928*a*) from Pebas is considered distinct because the axis of its v-shaped sculpture points in a more posteroventral direction, its ventral margin is more convex, and its umbones are situated relatively further forwards with the anterior of the shell being both smaller and lower than in *D. longulus*. *D. longulus* resembles the living *D. charruanus* (d'Orbigny 1835*a*) (d'Orbigny colln in BMZD) from Uruguay in outline, but the sculpture of the latter's umbonal region seems never to develop into the clear-cut v-shaped pattern of *D. longulus*. *D. ellypticus* Spix is also similar to *D. longulus*, but is less elongate. Its posterior margin is more rounded and is joined to the ventral margin by a curve of wider radius. In addition, it seems never to develop the clear-cut v-shaped sculptural pattern of the fossil species. A comparison with *Diplodon (Ecuadorea)* sp. aff. *bristowi* Parodiz is given on p. 273.

Parodiz (1969) tentatively placed *D. longulus* in *Triplodon* Spix, 1827 (type species the living *T. rugosus* Spix, 1827, by monotypy), but not only is it too elongate to conform with that genus but also lacks the convex ventral margin, the alate posterodorsal region and reverse v-shaped ribbing continuing onto the posteroventral ridge. However, Parodiz might well be correct in his suggestion that the fragmentary specimen, which Conrad described separately (1874*a*: 30; pl. 1, fig. 13) as a juvenile of *D. longulus*, was more likely to belong to *Triplodon rugosus*. Marshall (1928*a*) erected the new genus *Prodiplodon*, designating *P. singewaldi* as type species, but I agree with Parodiz (1969) in regarding this as one of the several synonyms of *Diplodon*. Parodiz' (1969) pl. 7, figs 2, 3 are copies (the latter trimmed) of Marshall's (1928*a*) pl. 1, figs 3, 6, which are two different views of the holotype of *P. singewaldi*. Plate 7, fig. 1 of Parodiz is a copy of Marshall's pl. 1, fig. 4, illustrating the holotype of *P. paucarpatensis* Marshall.

Diplodon sp. juv. Figs 303–305

Material studied. BMPD LL28105–7, Pebasian; Pichana, Peru (Hauxwell colln, extracted from matrix, 1982).

Dimensions. LL28105, lv, l, 1.76 mm. LL28106, rv, l, 0.96 mm. LL28107 lv, l, 1.02 mm.

Remarks. These three small specimens are all only the umbonal regions of shells, whose outlines are so badly damaged that their original shape can only be roughly deduced by examination of the growth lines. In consequence, the only measurement given above is the actual length of the specimen. All three possess well-preserved chevron sculpture characteristic of *Diplodon* but very rarely seen in adult shells in which the umbonal region is almost invariably eroded. Although these shells could conceivably belong to *D. longulus*, specific identification of such small specimens is quite impossible in the absence of a full growth series.

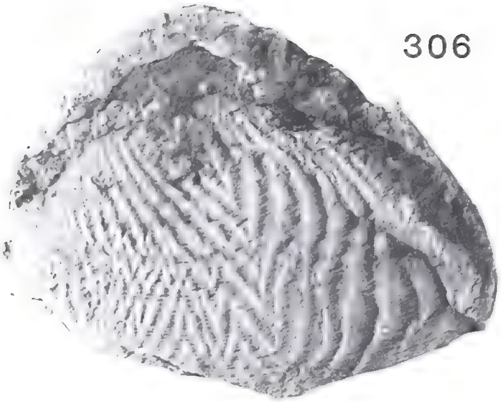
Subgenus ***ECUADOREA*** Marshall & Bowles, 1932

[= *Castalioides* Marshall, 1934; type species *Castalioides laddi* Marshall 1934, by original designation; Late Caenozoic, Venezuela].

(Figs 306–310)

Type species. *Ecuadorea bibliana* Marshall & Bowles, 1932, by original designation; Miocene, Loyola Formation, Ecuador. = *Diplodon liddlei* Palmer, *in* Liddle & Palmer 1941, a co-occurring species.

Diagnosis. Similar to *Diplodon*, s.str., in shape though generally less elongate; radial sculpture both stronger and more widespread than in *Diplodon*, s.str., often arranged in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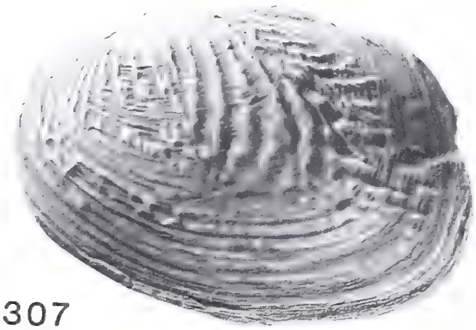
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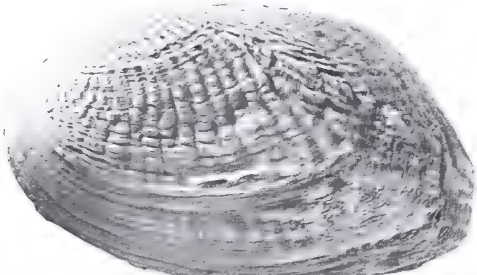
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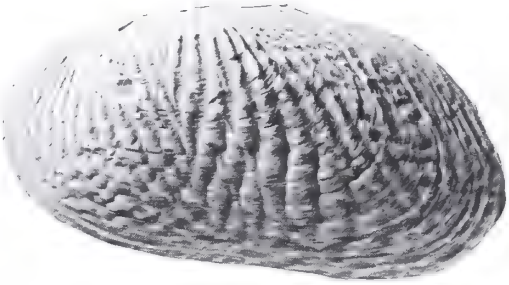
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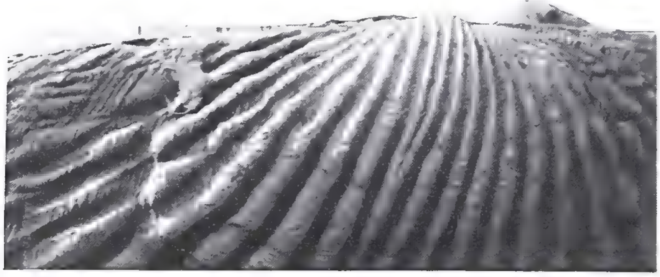


Fig. 306 *Diplodon (Ecuadorea) biblianus* (Marshall & Bowles). LL27807; left valve, × 2, of specimen whose right valve was figured by Bristow & Parodiz (1982: fig. 1) as *Diplodon (Ecuadorea) guaranianus biblianus*. Miocene, Loyola Formation; Loc. CRB 28, Cuenca Basin, Ecuador; Bristow Colln.

Figs 307–308 *Diplodon (Ecuadorea) guaranianus* (d'Orbigny). **307**, BMZD 1854.12.4.841; lectotype of *Unio guaranianus* d'Orbigny, figured by d'Orbigny (1846: pl. 69, figs 10–12). Recent; Rio Parana, Prov. Corrientes, Argentina, d'Orbigny Colln. Left valve, × 3. **308**, BMZD 1965169; holotype of *Unio fluctiger* Lea, figured by Sowerby (1868, species 229). Recent; unlocalized; Cuming Colln. Left valve, × 2.

Figs 309–310 *Diplodon (Ecuadorea) hylaeus* (d'Orbigny). **309**, BMZD 1854.12.4.843; lectotype of *Unio hylaeus* d'Orbigny, figured by d'Orbigny (1847: pl. 69, figs 8, 9). Recent; Chiquitos Province, Bolivia. Left valve, × 1.5. **310**, BMZD 1854.12.4.842; paralectotype. Recent; Santa Cruz de la Sierra Prov., Bolivia; d'Orbigny Colln. Umbonal region of right valve, × 5.

chevrons and sometimes reaching to ventral commissure, sometimes covering most of shell; dentition, as for genus; glochidia non-parasitic where known.

OTHER SPECIES ASSIGNED. Fossil: *Triplodon latouri* Pilsbry & Olsson, 1935; ? Miocene, La Cira Formation, Colombia. *Diplodon (Ecuadorea) bristowi* Parodiz, *in* Bristow & Parodiz 1982; Miocene, Loyola Formation, Ecuador.

Recent: *Unio guaraniana* d'Orbigny, 1835*a*; Rio Paraña, Argentina; = *Unio fluctiger* Lea, 1859; unlocalized. *Unio hylaea* d'Orbigny, 1835*a*; Province of Santa Cruz and Chiquitos, Bolivia. *Castalia pazi* Hidalgo, 1868; Imbabura, Ecuador.

DISTRIBUTION. Miocene to Recent, South America only.

REMARKS. *Ecuadorea* is unfortunately based on an indifferently preserved fossil species. The list of living species assigned does not claim to be exhaustive: all were included in *Diplodon* (s.str.) by Haas (1969*a*) who did not deal with genera based on fossil species. Nevertheless, *Ecuadorea* appears to be comparatively less common than *Diplodon*, s.str.

D. (E.) liddlei was described by Palmer (*in* Liddle & Palmer 1941: 48) from the same locality as *D. (E.) bibliana*. The distinctions made by her and later by Parodiz (1969: 66; Bristow & Parodiz, 1982: 27) do not appear to warrant specific separation. Parodiz (Bristow & Parodiz 1982: 25) also placed *Castalioides laddi* Marshall (1934) in synonymy of *D. (E.) bibliana*: *Castalioides* and *Ecuadorea* can certainly be accepted as generic synonyms. *C. laddi* came from strata in

Venezuela thought by Marshall to be Pleistocene. Later Palmer described the species from another locality thought (1945: 11) to be either Pliocene or Pleistocene, preferably Pliocene – in any event thought to be considerably younger than the Ecuadorean *D. (E.) bibliana*.

However, it is not accepted that the two species are the same. Marshall's (1934) illustrations of the holotype of *C. laddi*, in particular his fig. 1, clearly show a sculptural pattern rather similar to that of *D. (E.) hylaeus* d'Orbigny with the posterior ridge forming the axis of chevron ribbing, in addition to the signs of chevron ribbing in the region immediately ventral to the umbo. In *D. (E.) bibliana* the chevrons are perhaps stronger below the umbones but no chevron ribbing is associated with the posterior ridge.

Parodiz (1969: 62; Bristow & Parodiz 1982: 25) placed *Triplodon latouri* Pilsbry & Olsson, 1935 in *D. (Ecuadorea)* following the doubts originally expressed by its authors about its generic assignment (1935: 16). Its hinge is unknown and it lacks both the anterior and posterior alation of *Triplodon*. Its placement in *Ecuadorea* is accepted here. Even though its sculpture consists of extremely coarse chevrons, there is a certain resemblance between it and *D. (E.) pazi* (Hidalgo) (compare Parodiz, 1969: pl. 4, figs 4, 7, 8).

Parodiz (1969: 66; Bristow & Parodiz 1982: 25) regarded *D. (E.) biblianus* as a subspecies of *D. (E.) guaranianus* (d'Orbigny). This arrangement is not accepted here. It is clear from Parodiz' arguments that he had confused *D. (E.) guaranianus* with *D. (E.) hylaeus* (d'Orbigny). Haas (1969*a*: 519–520) also appears to have been somewhat confused as he regarded *D. pazi* as a subspecies of *D. guaranianus*, in spite of its greater resemblance to *D. hylaeus. D. guaranianus* and *D. hylaeus* had previously (Simpson 1900: 884) been regarded as synonyms. *D. (E.) hylaeus* may be described as the stronger, more angulated species, whilst *D. (E.) guaranianus* is the more slender, more ovate species, extremely thin-shelled with the ribs visible from the interior (i.e., the reverse of the distinctions given by Parodiz). Neither species resembles *D. (E.) biblianus* closely. Bonetto (1967: 71) placed *D. bibliana* in the synonymy of the living *D. pazi*: this is not accepted here.

Johnson (1971: 85) selected 'holotypes' and 'paratypes' of the two d'Orbigny species. Correctly, these should be referred to as lectotypes and paralectotypes. Both lectotypes are now figured to remove any remaining confusion: *guaranianus* Fig. 307, *hylaeus* Fig. 309.

The unlocalized holotype of *Unio fluctiger* Lea, 1859 (BMZD 1965169) (Fig. 308) was figured by Sowerby (1866: pl. 42, fig. 229 – quoted in his text as 299). Although considerably larger (l = 33.8 mm) than typical *guaranianus*, it appears to be a synonym.

Diplodon (Ecuadorea) sp. aff. ***bristowi*** Parodiz, *in* Bristow & Parodiz 1982 Fig. 311

MATERIAL STUDIED. BMPD LL27889, left valve; Late Caenozoic; Loc. 54, La Tagua (Eden colln).

DESCRIPTION. Damage to the single left valve consists of partial loss of shell outline as well as crushing which has somewhat distorted both the outline and sculpture. Nevertheless, examination of the commissure suggests that the shell is virtually complete and not merely the umbonal region of a larger specimen. The hinge is unknown. The shell has a relatively small height to length ratio, a rather tumid umbo, a slight well-rounded posterior angulation and strong, irregularly bifurcating radial ribbing. No chevron patterning can be observed. About 15 ribs can be counted on the anterior and ventral parts of the shell. They reach their maximum in both strength and numbers between 10 and 15 mm from the umbo. Although weaker in later growth stages, some can still be observed reaching the ventral commissure. Growth lines are not prominent, being typical of the genus: they clearly indicate the lack of both anterior and posterior alations.

DIMENSIONS. l = 28 mm; h = 24 mm; valve breadth = 8 mm.

REMARKS. Although the rather tumid umbo is also reminiscent of *Castalia*, this feature is present to a lesser extent in *D. (E.) bibliana*. This specimen is referred to *Diplodon (Ecuadorea)* on the character of its sculpture and lack of definite posterior angulation. The sculpture is both too strong and too persistent for *Diplodon*, s.str. It is also too irregular for *Rhipidodonta*, *Triplodon*, *Castalia* and *Chevronais*. The three last-named genera have strong to very strong posterior angulations, whilst *Triplodon* is also bi-alate. The unique holotype, LL27820, of *D. (E.) bristowi* Parodiz (*in* Bristow & Parodiz 1982: 26, fig. 2; Fig. 312 herein) is an external mould showing some details of the sculpture and a rather incomplete oval outline of a crushed shell, which, like the present specimen, had a prosogyrous umbo. The two are of about the same size, but *D. (E.) bristowi* differs in having about 30 comparatively weak but rather more regular ribs. *D. (E.) bibliana* differs from both by its chevron-patterned ribbing, shown clearly by the enlarged illustration of the holotype (Marshall & Bowles 1932: pl. 1, fig. 8) and by LL27807 (Bristow & Parodiz 1982: fig. 1). Two Pebasian species, *D. longulus* (Conrad) and *D. gardnerae* (Marshall), both placed in *Diplodon*, s.str., are not dissimilar to the La Tagua fossil. Both have strong sculpture and rather prominent umbones. Their sculpture, however, is chevron-patterned and dies away relatively close to the umbo. *D. (E.) guaranianus* is the most similar living species, but it is more elongate, its umbones are less tumid and its ribbing shows definite traces of chevron patterning. The ribbing of *D. (E.) hylaeus* and *D. (E.) pazi* are also much more regular.

Superfamily **MUTELACEA** Gray, 1847

[*nom. transl.* Parodiz & Bonetto, 1963: 205, *ex* Muteladae Gray, 1847: 197]

Family **MYCETOPODIDAE** Gray, 1840: 150

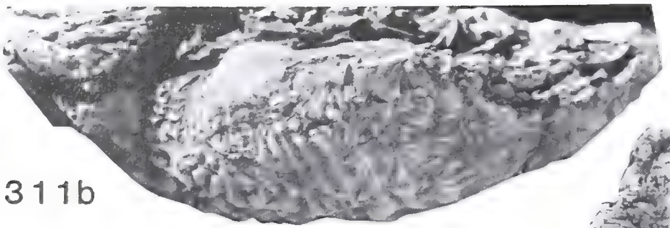
Subfamily **ANODONTININAE** Modell, 1942: 175

Haas (1969*a*: 548) attributed the Mutelidae to Conrad (1853: 267). Elsewhere, he also (Haas, *in* Moore 1969*b*: N446) credited Swainson (1840) with authorship of this family. Swainson, however, mentioned neither *Mutela* nor any suprageneric taxon based on it in his work.

Genus ***ANODONTITES*** (*sensu stricto*) Bruguière, 1792*c*.

[= *Ruganodontites* Marshall, 1931*a*, *b*; type species *Anodontites colombiensis* Marshall, 1921, by original designation; Recent, Colombia. *Haplothaerus* Conrad, 1874*b*; type species *H. capax* Conrad, 1874*b*, by monotypy; Late Caenozoic, Pebasian, Iquitos.]

(Figs 313–314)



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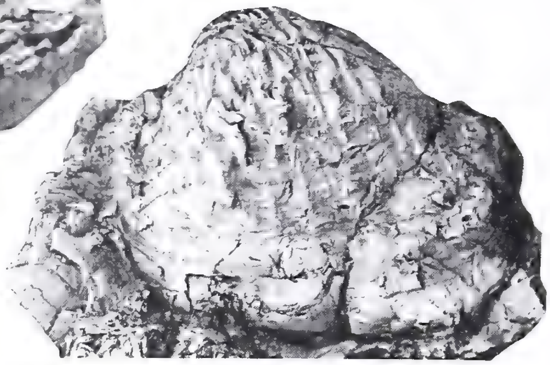

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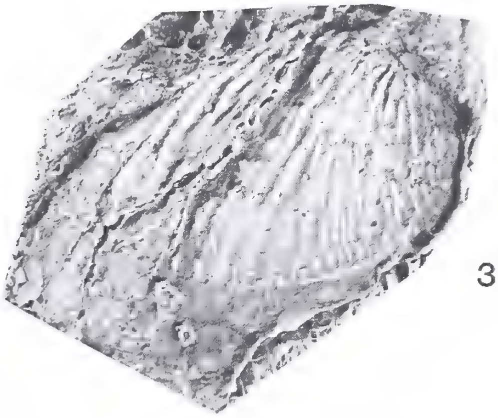


312

Fig. 311 *Diplodon (Ecuadorea)* aff. *bristowi* Parodiz. LL27889; Late Caenozoic; Loc. 54, La Tagua, Colombia; Eden Colln. a, left valve, × 2; b, dorsal view, × 3.

Fig. 312 *Diplodon (Ecuadorea) bristowi* Parodiz. LL27820; holotype, latex cast of external mould of right valve, × 2. Miocene, Loyola Formation; Loc. CRB 18, Cuenca Basin, Ecuador; Bristow Colln.

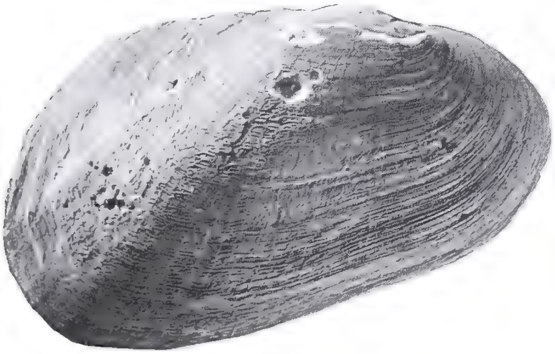


Fig. 313 *Anodontites crispata* Bruguière. Recent, type species of *Anodontites* Bruguière. BMZD 1984229; Ecuador, Geale Colln. Right valve, × 2.

TYPE SPECIES. *Anodontites crispata* Bruguière, 1792*c*, by monotypy. Recent, French Guiana (see Remarks).

DIAGNOSIS. Outline variable, elongate to oval; non-alate or incipiently alate; moderately inflated; periostracum smooth to scabrous, cloth-like, with microscopic radiating rays; shell surface unsculptured except for rare radiating riblets; edentulous; pallial line entire: muscle scars comparatively shallow; outer shell layer of coarse prisms, thickening towards shell margins.

SPECIES ASSIGNED. Fossil: (?) *Unio (?Anodon) totiumsanctorum* Hartt 1870, Palaeocene, Bahia Series; north-eastern Brazil (see Parodiz 1969: 14, 15, 84). *Anodon batesi* Woodward, 1871, Late Caenozoic, Pebasian; Pichana, Peru. *Haplothaerus capax* Conrad, 1874*b*, Late Caenozoic, Pebasian; Iquitos (Fig. 314). *Anodontites laciranus* Pilsbry & Olsson, 1935, ?Miocene, La Cira Formation; Middle Magdalena Valley, Colombia. *Anodontites olssoni* Palmer, *in* Liddle & Palmer 1941, Miocene, Biblián Sandstone; Cuenca Basin, Ecuador (see Bristow & Parodiz, 1982: 29).

Recent. Numerous species from South America (Simpson 1914: 1403–1457, Haas 1969*a*: 557–572).

GENERIC DISTRIBUTION. ?Palaeocene and Neogene to Recent, South America (see Remarks).

REMARKS. The conception herein of the genus follows that of Haas (1969*a*, *in* Moore 1969*b*) except that there seems little merit in treating *Ruganodontites* as being subgenerically distinct. Haas (1969*a*: 557) gives a fuller generic synonymy and (1969*a*: 562) a more detailed, but by no means complete, synonymy of the type species, *A. crispata* Bruguière (Fig. 313), whose type material came from Cayenne (French Guiana). His synonymy includes *Anodon reticulatus* Sowerby, 1867 and *Anodonta napoensis* Lea, 1868, thus implying that the species is also present in the Upper Amazon Basin. Haas' assertion that the species also occurs both in Rio La Plata, the Pacific drainage of Ecuador, and in the Magdalena river system of Colombia is probably incorrect. Although von Ihering (1893: 121) lists the species (as *Glabaris reticulata* 'Reeve') from the Amazon Basin, it does not appear in his other faunal lists covering Rio La Plata, Rio Paraguay and southern Brazil. The Colombian record may be based on the misidentification by Ortmann (1921: pl. 41, figs 2a, 2b, 3) of *A. colombiensis* Marshall. Parodiz (1969: 83) suggests that at the present day the genus is best known from north-eastern and central South America, and that west of the Andes it is unknown south of the Equator.

Several species of *Anodontites* have a very scabrous appearance. This feature appears to be confined to the periostracum and is absent on the underlying calcareous shell surface. The features of the outer prismatic layer given in the

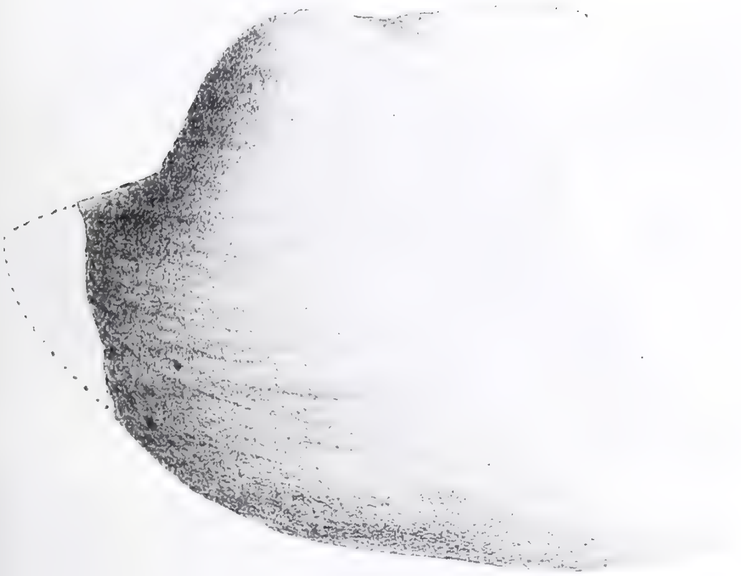


Fig. 314 *Haplothaerus capax* Conrad. Copy of type illustration at original size (Conrad 1874*b*: pl. 12, fig. 1). Pebasian; Iquitos; specimen presumed lost (*ex* ANSP). Magnification not known.

above diagnosis is, as explained on p. 264, probably also of superfamilial significance. At the very least, it may be used, as here, to distinguish between species of *Diplodon* and *Anodontites* which sometimes have very similar outlines.

Anodontites (Anodontites) batesi (Woodward, 1871)

Fig. 315

*v. 1871 *Anodon batesi* Woodward: 103, pl. 5, fig. 10.
*? 1874*a* *Anodonta pebasana* Conrad: 29, pl. 1, fig. 5.
1878 *Anodonta batesi* (Woodward) Boettger: 498.

HOLOTYPE. BMPD L27743, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln). Holotype of *A. pebasana* Conrad presumed lost, as not located in ANSP (Johnson & Baker, 1973: 165). No further material.

DISTRIBUTION. Late Caenozoic, Pebasian only, *A. batesi* as above; *A. pebasana* either Pebas, Old Pebas or Pichana (Conrad 1874*a*).

DIAGNOSIS. Elongate *Anodontites* with minute umbones hardly projecting above long, straight, hinge line; anterior and posterior margins both meeting hinge line at definite angle; posteriorly incipiently alate; ventral margin fairly straight, sloping downwards towards posterior; shell surface smooth except for growth lines; edentulous.

DESCRIPTION. The shell of the holotype and only available specimen is partly decorticated. Its outline is considerably modified due to damage to its anterodorsal and posterior regions. Study of growth lines shows that anteriorly the ventral margin curves smoothly upwards into the anterior margin, which eventually becomes recurved and meets the hinge line at a definite angular junction. Posteriorly, the ventral margin also forms a smooth curve with the posterior margin. The latter is rather truncated in the region of mid shell-height, before being recurved into an incipient alation. The junction with the hinge line is angular. The umbones are very small, pointed and prosogyrous. In both valves, the prodissoconch appears to be depressed in the region below the umbones. The outer prismatic layer is absent from large areas surrounding the umbones in both valves. A furrow running posteroventrally from the umbo is clearly visible in the nacreous layer, but is much fainter in the outer prismatic shell layer at about 20 mm from the right umbo. The shell is otherwise smooth except for growth lines. The outer prismatic layer thickens noticeably as it approaches the commissure (i.e. in the later growth stages of the shell). The hexagonal patterning formed by this layer is visible on much of the shell surface.

DIMENSIONS. In mm.	l	(e)l	h	br	l/h
Holotype, L27743	65.4	66.5	39.5	22.2	1.68(e)
A. pebasana (from Conrad's type illustration)	42.4	–	22.5	–	1.89

REMARKS. Woodward's excellent figure shows the shape of the growth lines clearly. He was unable to find (1871: 104) any South American species of comparable form in the British Museum collections (i.e., now BMPD). *A. batesi* is immediately distinguished from virtually all known *Anodontites* by the straightness of its hinge line and by how little the umbones project above it. It bears some resemblance to three species in particular: *A. crispata* Bruguière 1792*c*, *A. trapezialis* (Lamarck, 1819) and *A. colombiensis* Marshall, 1921. Extensive synonymies of *A. trapezialis* from the Rio Solimões are given by Haas (1969*a*: 568) and Fechter (1983*b*: 227); the latter also provided good illustrations (1983*b*: pls A, B) of two junior synonyms *A. giganteus* (Spix) and *A. anserinus* (Spix). None of these three species show traces of posterior alation. The anterior margins of both *A. crispata* and *A. colombiensis* merge smoothly into their hinge lines. Although the anterior margin of *A. trapezialis* meets the hinge line at a definite angle, it is more recurved from the vertical than in *A. batesi*. Both *A. trapezialis* and *A. colombiensis* have long, straight hinge lines and low umbones, whilst the umbones of *A. crispata* are fairly prominent. *A. trapezialis* and *A. crispata* are both less elongate than *A. batesi* and their umbones are situated more posteriorly. The ventral margins of *A. batesi*

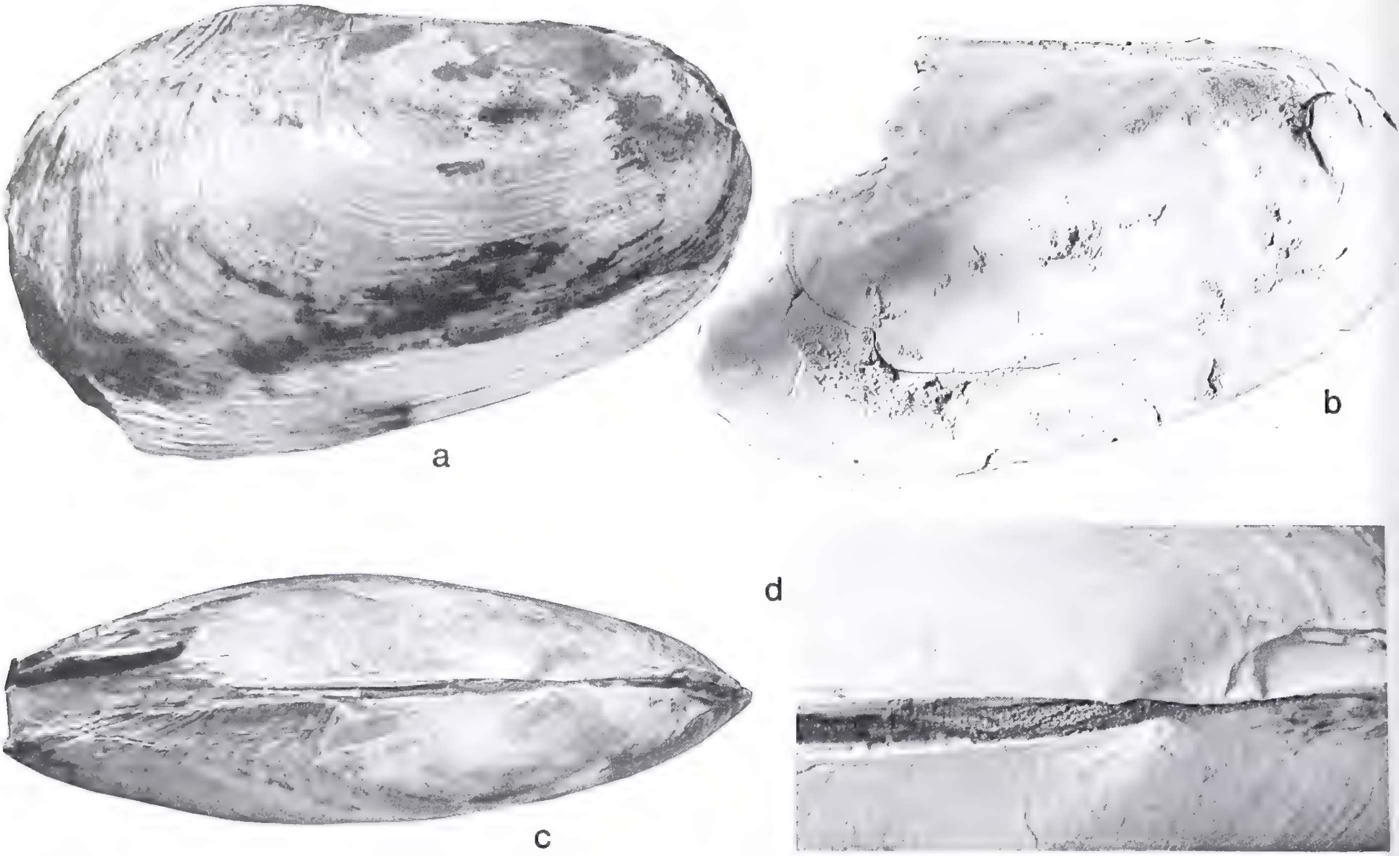


Fig. 315 *Anodontites batesi* (Woodward). L27743, holotype. Pebasian; Pichana, Peru; Hauxwell Colln. a, right valve exterior, × 1.5; b, left valve interior, dorsal view, × 1.5; c, dorsal view, × 1.5; d, umbonal region, × 4. See facing page.

and *A. crispata* are similar: both are comparatively straight and slope downward towards the posterior at about the same angle, though the ventral margin in *A. trapezialis* is more curved.

Conrad's (1874*a*) illustration of *A. pebasana* shows a shell with an outline very similar to that of *A. colombiensis*, but his description does not mention the waisting of the shell below the umbones which is such a distinctive feature of the latter species. *A. pebasana* is thus placed tentatively in the synonymy of *A. batesi*: both have remarkably small umbones and straight hinge lines. The only real differences appear to be that the ventral margin in *A. pebasana* is more parallel to the hinge than in *A. batesi* and that the latter is less elongate.

Parodiz (1969) did not deal with either species formally, but wrote (1969: 84) in his discussion of *Anodontites* that *A. pebasana* probably belonged to the genus, but was also probably likely to be based on a valve of a living species allied to *A. siliquosus* (Spix, 1827). That species lacks pointed umbones (Fechter 1983*b*: pl. E, figs 5, 6) and is best referred to *Mycetopoda* (Haas 1969*a*: 574). In the absence of Conrad's specimen, this point cannot be resolved, but the comparisons made herein strongly suggest that *A. pebasana* cannot be matched with any known living species and is therefore very likely to be fossil. The holotype of *A. batesi* is clearly a fossil, infilled with matrix typical of Pichana. Both valves of this edentulous species were in contact, as in life. This suggests that burial took place very shortly after death, which in turn implies that some truly fresh-water environment which could support naiades existed fairly close to Pichana. It is surprising that this specimen is the only naiad among over 1000 bivalves in Woodward's share of Hauxwell's collection. The only naiad in Conrad's (1871*b*) share of that collection was a 'bivalve related to *Mulleria*' which was apparently not worth illustrating.

Subclass **HETERODONTA** Neumayr, 1884
emend. von Martens, 1884
Order **VENEROIDA** H. & A. Adams, 1856

Superfamily **DREISSENACEA** Gray *in* Turton, 1840

[*nom. transl.* Gill (1871: 19) *ex* Dreissenadae (family) Gray (*in* Turton 1840: 277, 299)].

Family **DREISSENIDAE** Gray *in* Turton, 1840

[*nom. correct.* Gray (1840: 151) (see also ICZN, 1956, Direction 41)].

The suggested generic distribution of members of this superfamily, as outlined by Keen (*in* Moore 1969: N643–4) and Eames (*in* Morley Davies 1971: 244–5), and ideas on its evolution (Morton 1970), need considerable modification in the light of work by Andrussov (1897–8) which has been overlooked by some modern authors. His classification was basically similar to those of the present day in that *Dreissena* van Beneden, 1835, without a myophore, was separated from *Congeria* Partsch, 1835, which possessed one. However,

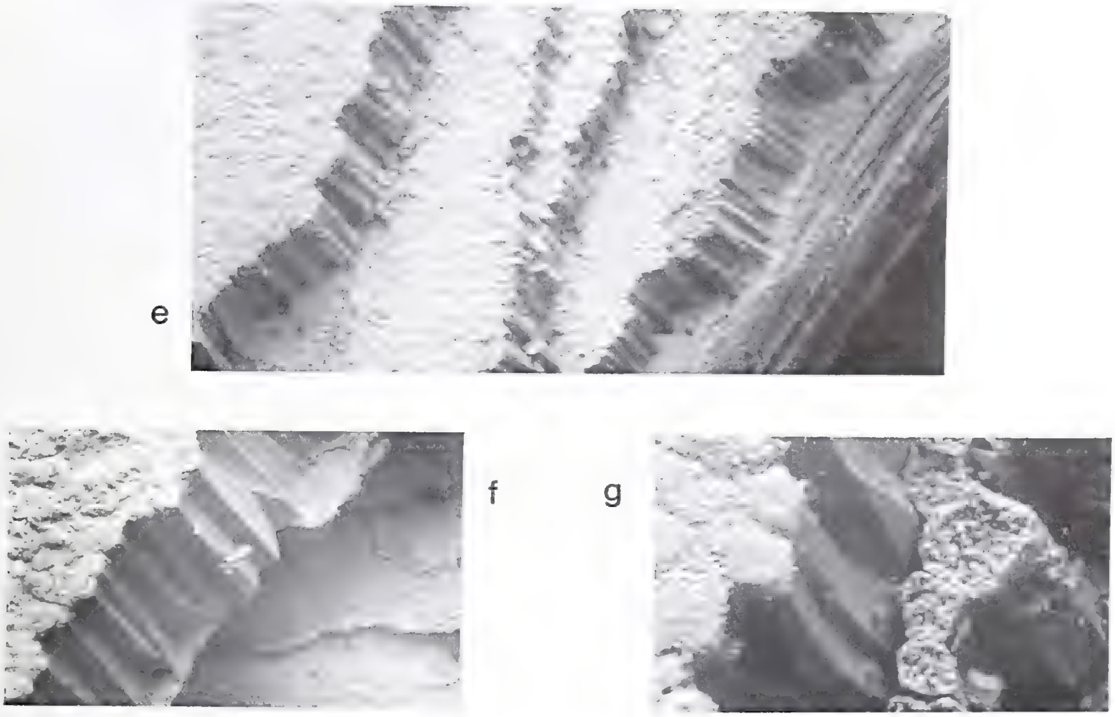
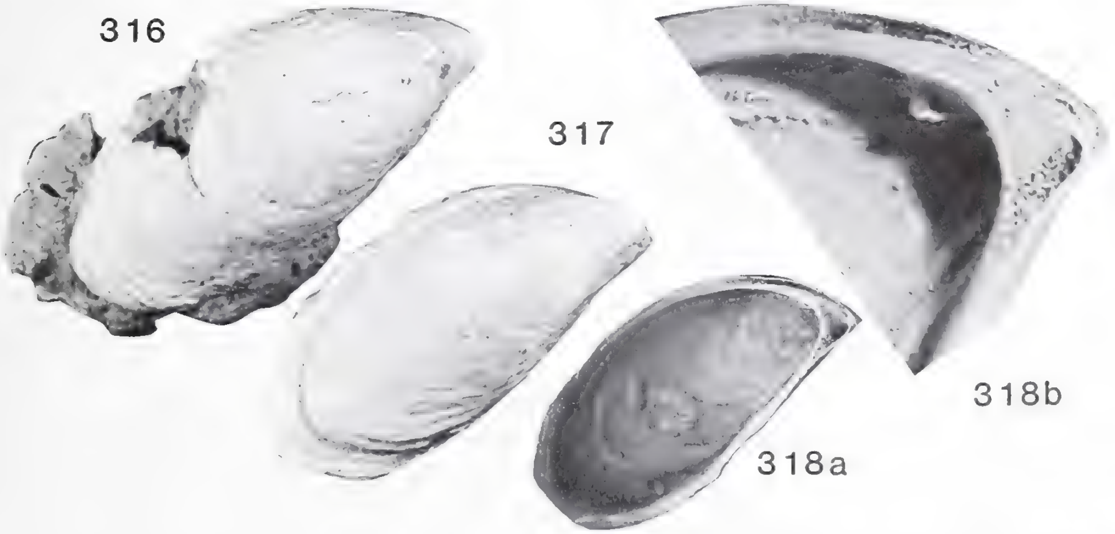


Fig. 315 *Anodontites batesi* (Woodward). L27743, holotype. Electron micrographs showing stout prisms overlying nacreous shell layer. e, × 65; f, × 130; g, × 340. See facing page.



Figs 316–318 *Mytilopsis sowerbyi* (d'Orbigny). Upper Eocene, Headon Beds, Priabonian; Hordwell, Hampshire, England. **316**, BMPD 43249; right valve external, × 4. Lectotype of *Mytilus sowerbyi* d'Orbigny, probably the specimen figured by J. de C. Sowerby (1826: *Min. Conchology* **6**: pl. 532, fig. 2) as *Mytilus brardi* 'Faujas'. **317**, LL28131, F. E. Edwards Colln; right valve external, × 4. **318**, LL28130, F. E. Edwards Colln. a, left valve internal, × 4; b, detail showing septum and apophysis, × 10.

Andrussov, who appears not to have been aware of the erection of *Mytilopsis* Conrad, 1858, which also has a myophore, divided *Congeria* into a number of 'groups' without status in nomenclature. Some have since been revised and described formally by Marinescu (1973), but none of these are of relevance to species under consideration herein. Andrussov's 'mytiliformes' (1898: 69 *et seqq.*) included the western hemisphere Recent species normally assigned to *Mytilopsis*, as well as *Dreissena fragilis* Boettger, 1878, from Pebas. Andrussov's 'modioliformes' (1898: 69, 172 *et seqq.*)

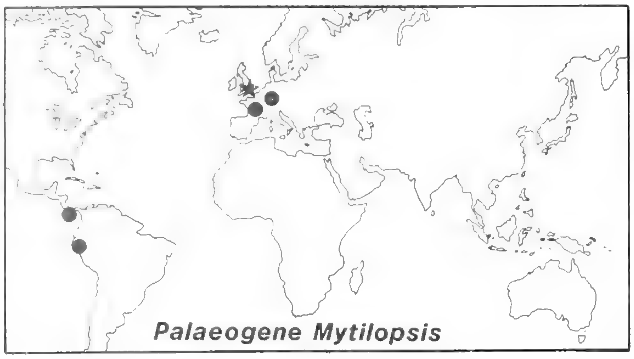


Fig. 319 Worldwide Palaeogene distribution of *Mytilopsis*. ★, Eocene record; ●, Oligocene records.

accommodated species with shapes rather similar to the 'mytiliformes' and included (1897: 175) several European Tertiary species such as *Dreissena sowerbyi* d'Orbigny, 1850 (Figs 316–318) from the Headon Beds of the English Eocene (Priabonian Stage). A re-examination of the type and other material of this species shows that it is not generically separable from *Mytilopsis*. Unnamed specimens in BMPD from Aquitanian and other mid-Tertiary horizons in France and Germany, as well as German material identified by D. Kadolsky (personal communication) as *Mytilopsis brardi* (Brongniart, 1823), confirm the basic soundness of Andrussov's observations.

It thus becomes apparent that *Mytilopsis* was far from rare in the European early to mid-Tertiary, and definitely occurs in the Upper Eocene of England. It also appears that during the late Neogene, *Mytilopsis* is replaced by *Dreissena* in Europe. This is in complete contrast to the generally accepted view that the European fossil species should all be placed in the living genus *Dreissena*, which allegedly first occured in the Eocene, whilst western hemisphere dreissenids should all be assigned to *Mytilopsis* occuring from the Upper Oligocene onwards. The earliest known western hemisphere occurrences of *Mytilopsis* appear to be the records from the Oligocene of Panama and western Peru discussed below. The fossil record, thus reinterpreted, suggests that both *Congeria* and *Dreissena* might be derived from *Mytilopsis*, rather than that *Mytilopsis* is descended in some way from *Dreissena* as has been previously held (Morton 1970).

A further consequence of this revision of the fossil history of *Mytilopsis* is that the numerous cases of its suspected introduction to new areas now need re-examination. As long as it was accepted that the genus was only found fossil in the western hemisphere, it was not reasonable to dispute that anomalous Recent records from Europe, west Africa, Fiji and India were all the result of introductions from the western hemisphere, where the genus was endemic. Morton's tentative hypothesis (1981: 26) that *M. sallei* (Recluz) may have migrated to Fiji *via* the Panama Canal since its completion in 1914 can be questioned on three grounds. First, Dall (1898: 809) had already recorded the genus (as *Congeria*) from Fiji. Secondly, the Panamanian and western Peruvian fossil records from the western part of the Panamic Pacific province during the mid-Tertiary are from areas separated from Fiji only by ocean, and, in any case, considerably predate the land bridge joining South and Central America. Thirdly, Recent species of *Mytilopsis* had already been described by the late 19th Century from the Pacific coast of Colombia and Ecuador (Keen 1971, Olsson 1961, discussed under *sallei*, p. 284): their ancestors must have reached that region before the formation of the land bridge.

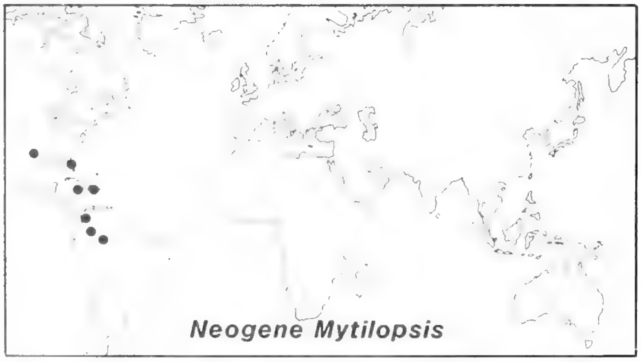


Fig. 320 Western Hemisphere Neogene distribution of *Mytilopsis*.

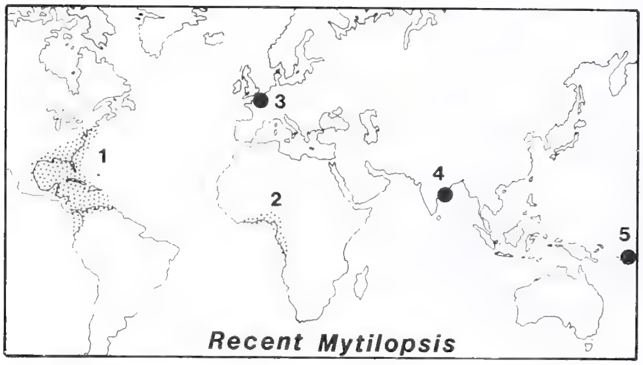


Fig. 321 Worldwide Recent distribution of *Mytilopsis*. 1, Western hemisphere; 2, West Africa (Pilsbry & Becqueart 1927, Binder 1968), probably introduced; 3, Rhine–Scheldt Delta (Adam 1960, Wolff 1969); 4, India (Morton 1981); 5, Fiji (Hertlein & Hanna 1949). 3, 4 and 5 almost certainly introduced.

Genus *MYTILOPSIS* Conrad, 1858

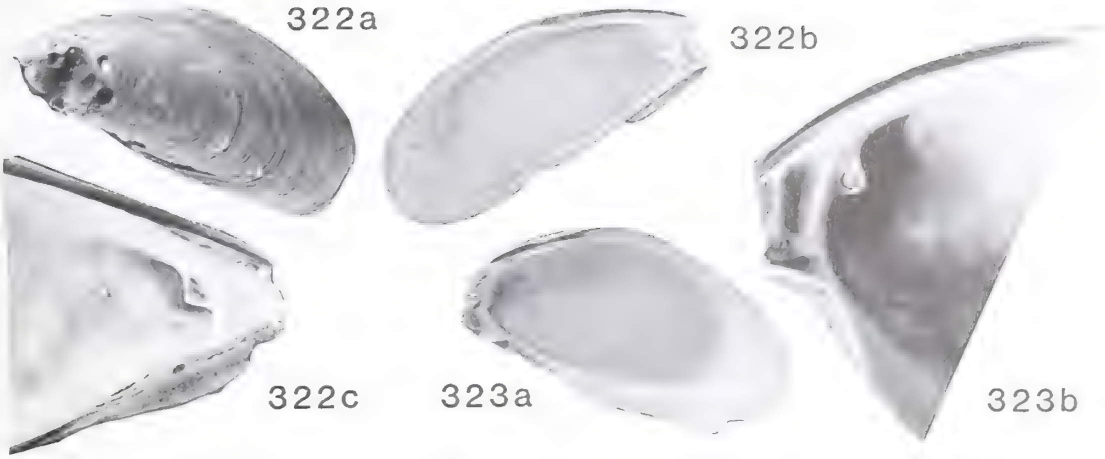
[= *Praxis* H. & A. Adams, 1857: 522, *non* Guenée, 1852: 28 (Lepidoptera). Although several bivalve species were originally listed under *Praxis*, no type designation has ever been made.]

Type species. *Mytilus leucophaetus* Conrad, 1831: 263. Recent, eastern United States, Hudson River to Gulf Coast. By subsequent designation of Dall, 1898: 808.

Diagnosis. Rather small mytiliform dreissenid; apophysis present.

Other species assigned. Recent: other species recognized herein from the western hemisphere are *Dreissena sallei* Recluz, 1849, Caribbean, and *Septifer trautwineana* Tryon, 1866*b*, Pacific drainage, northern South America. All other nominal living species appear to fall into the synonymy either of *M. sallei* (see Marelli & Gray 1983, and p. 280 herein), *M. trautwineana* (see Olsson 1961, Keen 1971) or *M. leucophaetus* (see Marelli & Gray 1983).

Fossil: *Dreissena scripta* Conrad, 1874*a*, Late Caenozoic, upper Amazon Valley, is the only extinct western hemisphere species recognized herein as distinct. Other species include



Figs 322–323 *Mytilopsis leucophaetus* (Conrad). BMZD 1984239; Recent; Green Cove Springs, Black Creek (tributary of St John's river), Florida; attached to submerged wood, collected live 28. 6. 1983 by Messrs Dan C. Marelli & Michael J. Greenberg. **322**a, b, left valve external, internal, both × 3; c, detail showing septum and apophysis, × 10. **323**a, right valve internal, × 3; b, detail, × 10.

Dreissena sowerbyi d'Orbigny, 1850, Upper Eocene, England and *Mytilus brardi* Brongniart, 1823, Aquitanian, Europe.

GENERIC DISTRIBUTION. Fossil: Eocene–Miocene; western Europe. Late Oligocene; Panama and Pacific drainage, Peru. Neogene; Amazon, Caqueta and Magdalena Basins of northern South America, Caribbean and southern United States (Florida and Texas).

Recent (endemic): eastern seaboard, United States; Gulf of Mexico; Caribbean; Pacific coast, Panama to northern Ecuador. Recent (? introduced): Rhine–Scheldt delta (Adam 1960, Wolff 1969); west Africa (Pilsbry & Becquaert 1927: 455–7); Panama; Fiji; India (Morton 1981).

REMARKS. In this paper fossil occurrences of *M. sallei* Recluz are recognized for the first time. Those Pebasian fossils, from the Upper Amazon Valley and other South American localities, which cannot be matched with any living specimens are assigned to the extinct *M. scripta* (Conrad).

Both Keen (*in* Moore 1969: N644) and Eames (*in* Morley Davies 1971: 245) recorded the genus as living in Asia, and it is probable that they were both following Dall (1898: 809) who stated that *Congeria* occurred in China. There appears to be no evidence for this. Morlet (1884: 402) described *Dreissena crosseana* and (1892*a*: 85; 1892*b*: 329) *D. massiei* from Cambodia: examination of these (in BMZD) shows that they belong to *Sinomytilus* Thiele, 1934 (Mytilacea).

The shape of *Mytilopsis* is very simple, with few tangible diagnostic features, and because it is bysally attached and often lives crowded together, it tends to be variable. As a result, a considerable number of nominal species have been erected. Recently, however, our understanding at specific level has improved considerably following work on the Recent Pacific drainage species (Olsson 1961), the very comprehensive study of *M. leucophaetus* (Conrad) and *M. sallei* (Recluz) by Marelli & Gray (1983) and the increasing recognition that *Mytilopsis* has been introduced from the western hemisphere to other regions (Morton 1981). The resulting discontinuous geographical distribution patterns had led to a proliferation of specific names. This is analogous to the way in which new fossil species tend to be erected whenever the fauna of an isolated locality is described. De Greve (1938) was the only author dealing with South American fossil specimens who attempted to evaluate his material by comparing it with that already described from other deposits. It has been possible to take this process considerably further here, as is shown by the synonymies of *M. scripta* Conrad (p. 285) and *M. sallei* (pp. 280–2).

The recognition that *M. trigalensis* Olsson from the Oligocene of western Peru belongs to *M. scripta* and that the living Caribbean *M. sallei* occurs fossil in the Upper Amazon Basin is of interest when considering the Neogene palaeogeography of the region, but it would be dangerous to draw too firm conclusions. The Oligocene occurrences of the genus in Panama and western Peru, when the extended Tertiary Caribbean Province was in existence, mean that an invasion of the Upper Amazon region from the west cannot be ruled out. The great stratigraphical range of the species and the even greater range of the genus means that little can be deduced from it about the age of the Pebasian deposits. The fact that it is not the only living species in the fauna is, however, of some significance.

Marelli & Gray (1983) discussed the various diagnostic features by which *M. leucophaetus* and *M. sallei* might be separated. Of most potential use to palaeontologists are those which are likely to be shown by fossils. These include the more elongate shape of the former species and the differences between the septum and apophysis in the two species. In the former the apophysis is rather broad and is attached more to the rear margin of the septum than to the dorsal edge or hinge of the shell. In the latter species the apophysis is lanceolate and lies almost parallel to the dorsal margin of the shell to which it is attached. Its anterior, pointed, end tends to lie under the dorsal edge of the septum. The apophysis of *M. scripta* resembles that of *M. sallei*. Marelli & Gray's (1983) treatment of *M. leucophaetus* appears to be basically correct. However, *M. americana* (Dunker) is here transferred to *M. sallei*, whilst the holotype (BMZD, Cuming Colln) of *Mytilus tenebrosus* Reeve (1858: pl. 10, fig. 46), which was said to be from the Mississippi, is almost certainly the same specimen that Dunker (1853: 14) described as *Dreissensia cumingiana*. It is clearly a specimen of the European *Dreissena polymorpha* (Pallas). Two fossil occurrences of *M. leucophaetus* are discussed below.

Congeria lamellata Dall (1898) was described from the Plio-Pleistocene Caloosahatchee Formation of Florida. Dall stated that it was more elongate than the living *Congeria rossmassleri*

(Dunker) – here placed in *M. sallei* – and also had a different hinge. Unfortunately, he did not elaborate on this, and his illustrations of the internal features show no distinguishing features. BMPD LL28109–29, (Sowerby & Fulton Colln, 1899) from the Caloosahatchee Formation are allegedly of this species and are preserved in a white limestone. Some of the shells have been developed to show the internal features. Both these and the external shape suggest that a mixture of *M. leucophaetus* and *M. sallei* is present. Clearly, the true identity of Dall's species cannot be resolved without examining his type material. Both these species have been identified as living in Florida (Marelli & Gray 1983) and it is possible that Dall's species is unnecessary. Certainly, the majority of the thoughts that he expressed on the Dreissenacea in this particular paper cannot be accepted without rigorous checking.

Mytilopsis jamaicensis Woodring (1925: 86; pl. 10, figs 13, 14) was based on a single left valve from the Bowden Shell Bed of Jamaica; this is now dated as Pliocene, N19/20 (Blow 1969: 295–297, text-figs 27–29). The dorsal margin is comparatively short, about a third of the shell length. From the external appearance and Woodring's description and comments, it would appear that this species is very close to, if not synonymous with, *M. leucophaetus*. The record suggests that the fossil occurrence of this species extends south of its present-day range.

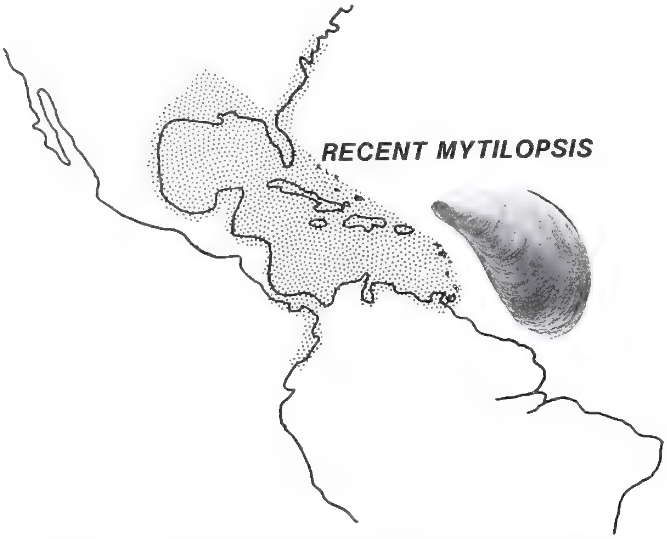


Fig. 324 Recent western hemisphere distribution of *Mytilopsis*. Inset: *M. sallei* (Recluz), eastern Mexico. × 1.5.

ECOLOGICAL DATA. *Mytilopsis* is usually found in brackish to fresh water. It occurs in lagoons in west Africa (Binder 1968), and in the western hemisphere. Keen (1971: 114) summarized the occurrence of *M. adamsi* Morrison in fresh water lagoons of San José Island, Panama. Marelli & Gray (1983: 192) report a rather similar distribution for *M. sallei* in coastal lakes and streams, but point out that little is known about its life cycle and factors affecting its distribution. It is often highly gregarious, living byssally attached to the substrate and other shells and nestling in small holes. Salinity tolerance is very high, ranging from fresh-water to supersaline (0–50 ‰). Tolerance to changes in temperature are also high (Escarbassière & Almeida 1976, Sidall 1980, Marelli & Gray 1983). Morton (1981: 37–39) also draws attention to characteristics, such as extensible siphons, ability to close the valves and efficient cleansing internal currents, which enable *M. sallei* to cope with a high sediment load.

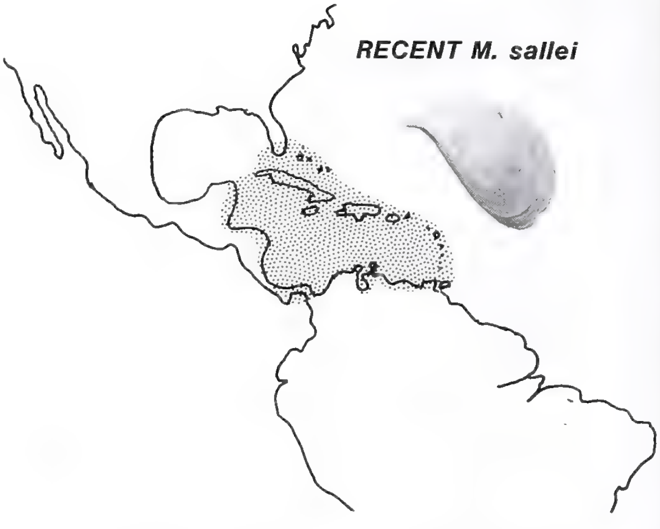


Fig. 325 Recent western hemisphere distribution of *M. sallei* (Recluz). Inset: *M. sallei* (Recluz), eastern Guatemala. × 1.5.

These characters are in keeping with a genus which is normally associated with wide seasonal variations in both salinity and temperature, and explain its ability to invade many Caribbean islands and the Pearl Islands off the Pacific coast of Panama, and to be introduced to other continents, with, or even without, the help of shipping. It is well suited to stretches of water near tropical coasts where salinities and water levels – and hence water temperatures – are likely to vary considerably between the rainy and dry seasons.

Apart from the rare records of *Mytilopsis* in marine faunas (Miocene of Dominican Republic, Maury 1917, and *M. jamaicensis* Woodring, 1925, known only from a single valve), the western hemisphere fossil occurrences of the genus are in faunas indicating reduced salinity, with the genus forming a substantial proportion of the biota.

Mytilopsis sallei **(Recluz, 1849)** Figs 327–344

* 1849*a* *Dreissena sallei* Recluz: 69.
. 1852 *Dreissena sallei* Recluz: Recluz: 255; pl. 10, fig. 10.
* 1852 *Dreissena domingensis* Recluz: 255; pl. 10. fig. 8.
* 1853 *Tichogonia rossmassleri* Dunker: 89.
1853 *Tichogonia sallei* (Recluz) Dunker: 91.
* 1853 *Tichogonia riisei* Dunker: 91.
1855 *Dreissenia rossmassleri* (Dunker) Dunker: 17.
1855 *Dreissenia sallei* Recluz; Dunker: 18.
* 1855 *Dreissenia morchiana* Dunker: 18.
1855 *Dreissenia riisei* (Dunker) Dunker: 19.
*. 1855 *Dreissenia americana* Recluz MS *in* Dunker: 19.
1855 *Dreissenia domingensis* Recluz; Dunker: 20.
1857 *Dreissena (Praxis) domingensis* Recluz; H. & A. Adams: 522.
1857 *Dreissena (Praxis) morchiana* Dunker; H. & A. Adams: 522.
1857 *Dreissena (Praxis) rossmaessleri* Dunker; H. & A. Adams: 522.
1857 *Dreissena (Praxis) riisei* (Dunker); H. & A. Adams: 522.

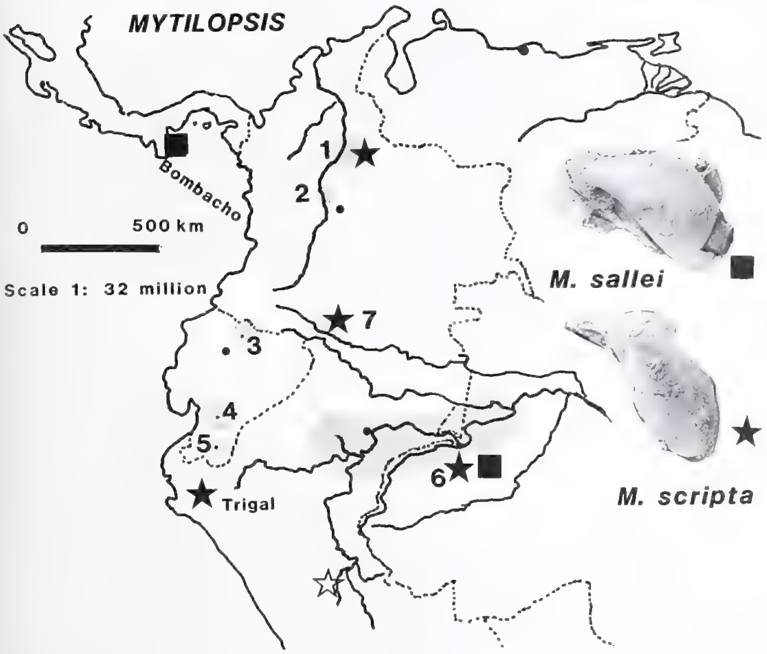
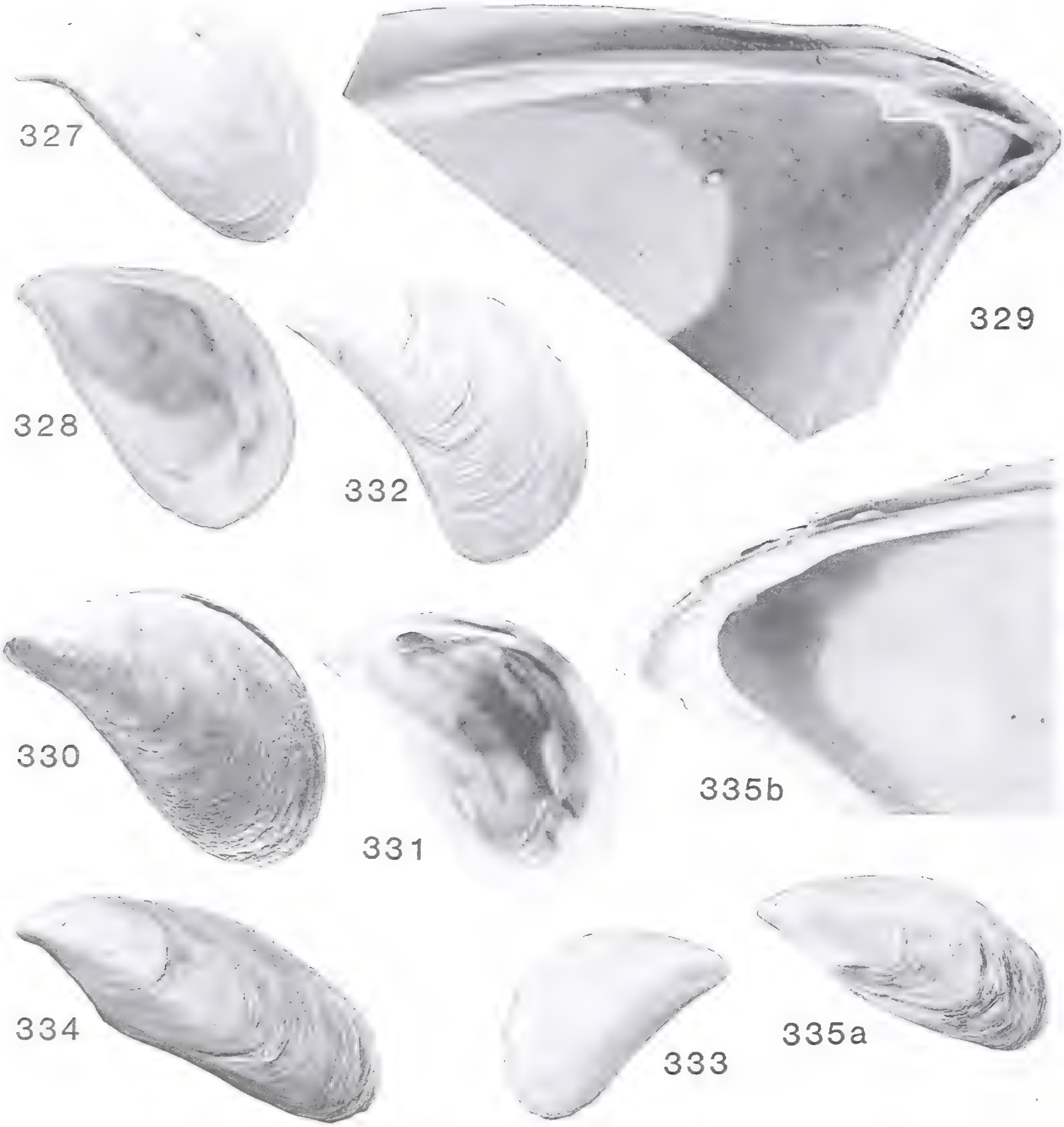


Fig. 326 Tertiary South and Central American distribution of *Mytilopsis*. Key as for Fig. 6 (p. 177). ■, *M. sallei* (Recluz); ★, *M. scripta* (Conrad); ☆ unconfirmed record. Inset: top, *M. sallei*, Canamá; bottom, *M. scripta*, Pichana. Both × 1.5.

1857 *Dreissena (Praxis) sallei* Recluz; H. & A. Adams: 522.
*v 1858 *Mytilus americanus* (Recluz MS) Reeve: pl. 10, fig. 43.
v. 1858 *Mytilus sallei* (Recluz) Reeve: pl. 10, fig. 44.
v. 1858 *Mytilus rossmassleri* (Dunker MS in Mus. Cuming (*sic*)) Reeve: pl. 10, fig. 45.
v. 1858 *Mytilus domingensis* (Recluz) Reeve: pl. 10, fig. 48.
v. 1858 *Mytilus morchianus* (Dunker) Reeve: pl. 10, fig. 51.
. 1858 *Dreissena americana* (Reeve) Fischer: 131.
1858 *Dreissena rossmassleri* (Dunker); Fischer: 132.
1858 *Dreissena morchiana* Dunker; Fischer: 132.
1858 *Dreissena sallei* Recluz; Fischer: 133.
. 1862 *Dreissena (Praxis) sallei* Recluz; Chenu: 157, fig. 782.
* 1878 *Dreissena fragilis* Boettger: 497 (*pars*); pl. 13, fig. 17, (? figs 16, 18).
. 1886 *Tichogonia sallei* (Recluz); Küster & Clessin: 17; pl. 12, figs 13, 14.
. 1886 *Tichogonia americana* (Dunker) (*sic*) Küster & Clessin: 28.
. 1886 *Tichogonia (Praxis) morchiana* (Dunker) Küster & Clessin: 18; pl. 12, figs 11, 12.
. 1886–7 *Tichogonia (Praxis) riisei* Dunker; Küster & Clessin: 25 (1886); pl. 15, figs 12, 13 (1887).
. 1886–7 *Tichogonia rossmaesleri* Dunker; Küster & Clessin: 27 (1886); pl. 15, fig. 77 (1887).
. 1886–7 *Tichogonia domingensis* (Recluz) Küster & Clessin: 26 (1886); pl. 15, fig. 14 (1887).
. 1894 *Dreissensia sallei* Recluz; Fischer & Crosse: 504, pl. 42, figs 4, 4a, 5, 6.
. 1897 *Congeria domingensis* (Recluz) Andrussov: 136; text-fig. 13B (p. 659).
. 1897 *Congeria riisei* (Dunker) Andrussov: 137; text-fig. 13F (p. 659).
. 1897 *Congeria rossmassleri* (Dunker) Andrussov: 138; pl. 20, figs 3–5; text-fig. 13C (p. 659).
. 1897 *Congeria sallei* (Recluz) Andrussov: 139; pl. 20, figs 3–5; text-fig 13E (p. 659).
. 1897 *Congeria morchiana* (Dunker) Andrussov: text-fig. 13A (p. 659).
*. 1898 *Congeria lamellata* Dall: 809 (*pars*); pl. 35, figs 13, 15 (?).
. 1900 *Dreissena sallei* Recluz; von Martens: 477; pl. 32, figs 4, 5.
*v 1906 *Dreissensia dalli* Clerc *in* Joukowsky & Clerc: 171; pl. 6, figs 1–5.
. 1917 *Mytilopsis domingensis* (Recluz) Maury: 195; pl. 39, fig. 5.
. 1924 *Dreissena acuta* Etheridge; Roxo: 44 (*pars*), figs A1, A2, A′1, A′2 (*non* figs A3, A4, A′3, A′4).
. 1938 *Congeria fragilis* (Boettger) de Greve: 49 (*pars*); pl. 9, fig. 15 (*non* figs 8, 14, 15).
. 1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. II de Greve: 54; pl. 9, figs 23–25, 27.
. 1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. III de Greve: 54; pl. 9. fig. 26.
* 1946 *Mytilopsis adamsi* Morrison: 46; pl. 1, fig. 4.
* 1949 *Mytilopsis allyneana* Hertlein & Hanna: 14; pl. 4, figs 5–8.
. 1964 *Mytilopsis leucophaetus* (Conrad); Weisbord: 206; pl. 27, figs 11, 12.
1975 *Mytilopsis sallei* (Recluz) Jones & Rutzler: 57 *et seqq*.
. 1976 *Mytilopsis sallei* (Recluz); Escarbassiere & Almeida: 165 *et seqq*.; figs 2, 4–8, 14.
v. 1978 *Mytilopsis sallei* (Recluz); Marelli & Berrend: 144.
v. 1981 *Mytilopsis sallei* (Recluz); Morton: 25 *et seqq*.; figs 1–12.
. 1981 *Mytilopsis allyneana* Hertlein & Hanna; Morton:



Figs 327–334 *Mytilopsis sallei* (Recluz). Recent; western hemisphere. **327**, BMZD 1984230; left valve external, × 2.5. Shell figured as *Mytilus sallei* (Recluz) by Reeve (1858: pl. 10, fig. 44); Central America; Cuming Colln. **328**, BMZD 1984230; right valve internal, × 2.5; shell from same sample as Fig. 327. **329**, BMZD 1984230; left valve internal showing septum and apophysis, × 10; shell from same sample as Fig. 327. **330**, BMZD 1984231; left valve, × 2.5; Laguna Bacalar, eastern Mexico; D. C. Marelli Colln. **331**, BMZD 1984231; right valve interior, × 2.5; same sample as Fig. 330. **332**, BMZD 1984233; left valve, × 2.5; shell figured as *Mytilus rossmassleri* (Dunker *MS* in *Mus. Cuming*) by Reeve (1858: pl. 10, fig. 45), labelled (erroneously) 'United States'; Cuming Colln. **333**, BMZD 1984235; right valve, × 4; shell labelled as *Mytilus riisei* Dunker; Vieque Island; Cuming Colln. **334**, BMZD 1984236; left valve, × 2.5; shell figured as *Mytilus domingensis* (Recluz) by Reeve (1858: pl. 10, fig. 48); Dominican Republic; Cuming Colln.

Fig. 335 *Mytilopsis africanus* (van Beneden). BMZD 1984238: a, left valve external, × 1.5; b, right valve internal showing septum and apophysis below, × 4. Shell figured by Reeve (1858: pl. 10, fig. 47); Recent; Senegal; Cuming Colln.

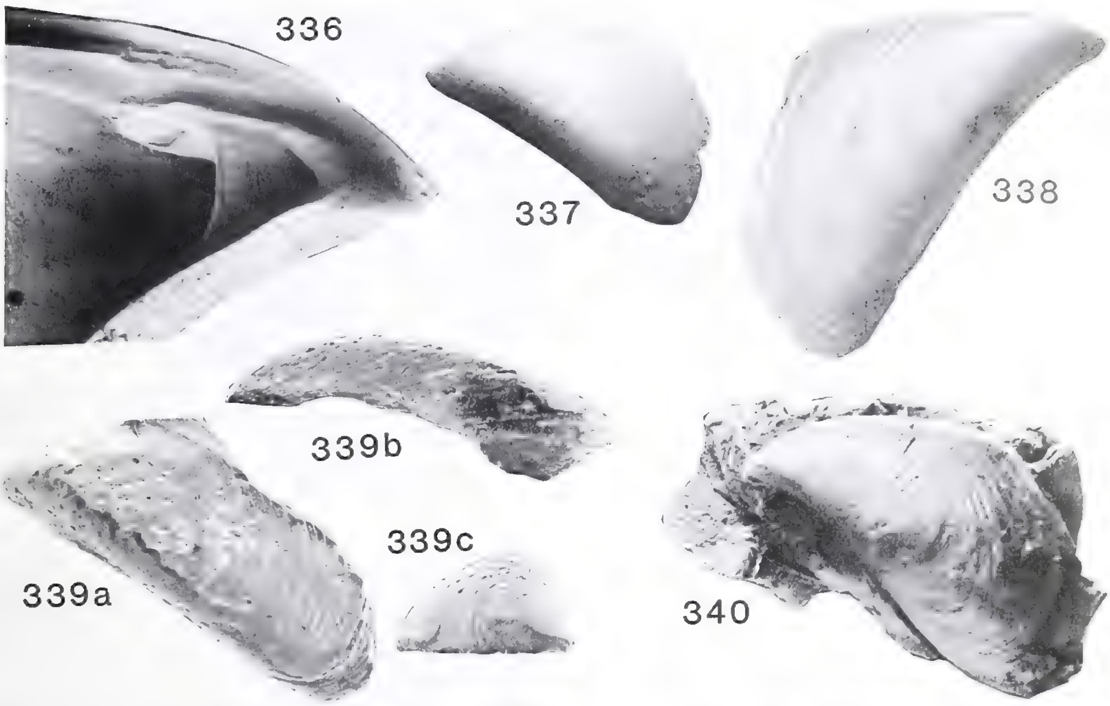
26 *et seqq*.; fig. 12c.

1983 *Mytilopsis sallei* (Recluz); Marelli & Gray: 189, figs 5, 6, 8.

TYPE MATERIAL. Types of *Dreissena sallei* Recluz not studied. Recent, Rio Dulce d'Izabel, Guatemala (Salle Colln; Recluz, 1849*a*).

Lectotype, selected herein, of *Dreissensia dalli* Clerc *in* Joukowsky & Clerc 1906, the shell originally figured as pl. 1, figs 4, 5. The three other specimens, the originals of pl. 1, figs 1, 2, 3, and over thirty unfigured specimens, are paralectotypes. All ? Late Oligocene (originally dated as Miocene or Pliocene), Bombacho, western Panama (Joukowsky Colln, Geneva N.H.M.)

?Syntypes of *Dreissenia americana* Dunker, 1855. Recent. Both Dunker and Reeve (1858) attributed the species to Recluz 'MS'. All three workers were almost certainly basing this species on the four shells in Cuming's Colln (BMZD



Figs 336–340 *Mytilopsis sallei* (Recluz). Pebasian; Peru and Colombia. **336–338**, Pichana; Peru; Hauxwell Colln. **336**, LL28097; left valve internal, showing septum and apophysis, × 12. **337**, LL28099; juvenile left valve, × 10. **338**, LL28098; juvenile right valve, × 10. **339**, LL27966; Puerto Nariño, Colombia; Weeda Colln. a, left valve external, × 10; b, side elevation of long diagonal anteroventral edge, × 10; c, front view, × 6. **340**, LL27915; Canamá, Peru; left valve, × 3; specimen found under holotype of *Dreissena acuta* Etheridge; Barrington Brown Colln.

1984237). They are so small that it is impossible to tell which shell Reeve figured. (*Mytilus americanus* d'Orbigny, 1846: 648 is not this species.)

Other material studied. Fossil: Late Caenozoic, Pebasian. LL27957, LL27933, LL28096–99, Pichana, Peru (Hauxwell Colln, extracted from matrix, 1982); LL27915, Canamá, found (in 1982) with holotype of *Dreissena acuta* Etheridge (see p. 285; Barrington Brown Colln); LL27966, Puerto Nariño, Colombia (Weeda Colln); LL28109–19, as *Congeria lamellata* Dall, Late Caenozoic; Caloosahatchee, Florida (Sowerby & Fulton Colln, 1899).

Recent (All BMZD): Cuming Collection samples generally of three or four shells and including the specimens figured by Reeve (1858) of various nominal species. *M. sallei* Recluz, 'Central America' (BMZD 1984230); *M. rossmassleri* 'Dunker MS in Mus. Cum., United States' (BMZD 1984233); *M. morchiana* Dunker, unlocalized (BMZD 1984234); *M. riisei* Dunker, Vieque Island (BMZD 1984235). Numerous specimens, 1.5 – 2.0 m depth, in scattered clumps, Quintana Roo, Laguna Bacalar, Mexico (Marelli & Berrend 1978) (Marelli Colln; BMZD 1984231). Six shells, labelled '*M. sallei*, Rio Dulce d'Izabel' (Cuming Colln; BMZD 1984232). Various other samples labelled 'Guatemala', including 93.2.4.2048–9. Specimens labelled *M. africana* (van Beneden), from Senegal (BMZD 1984238) are possibly synonymous. See p. 284.

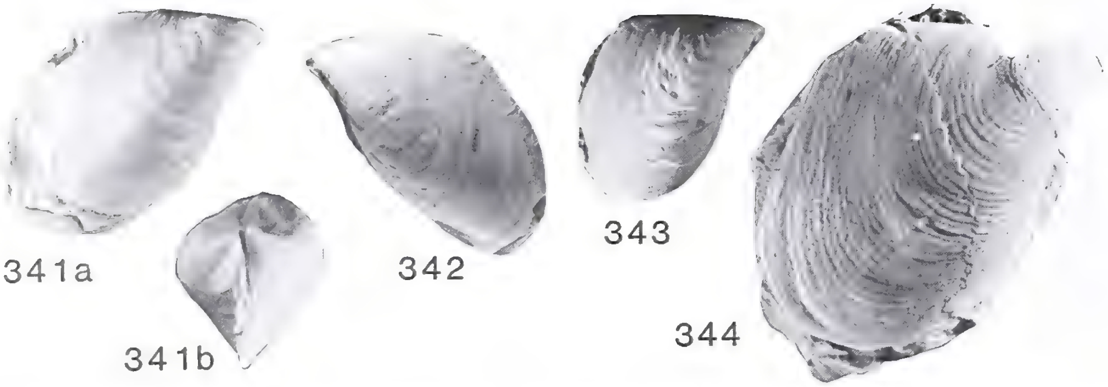
Further records. Fossil: Upper Miocene, Cercado Formation, Dominican Republic (Maury 1917). Late Caenozoic, Florida (Dall 1898). Raised beach, Venezuela (Weisbord 1964). Late Caenozoic, Pebasian; Pebas, Peru (Boettger 1878); Iquitos, Peru (de Greve 1938); Três Unidos, Peru (Roxo 1924).

Recent. In the following entries, a specific name coupled with that of an author denotes that the reference is to the type locality of the nominal species: Guatemala (Fischer & Crosse 1894); Guatemala and Honduras (Dunker Colln, von Martens 1900); St Thomas Isle, W. I. (Dunker 1853, as *T. riisei*; Dunker 1855, as *D. morchiana*); Unare lagoon, Anzoategui State, Venezuela, 10° 10′ N, 65° W, (Escarbassiere & Almeida 1976); locks of Panama Canal (Jones & Rutzler 1975); Fiji (Hertlein & Hanna 1949, as *M. allyneana*); Visakhapatnam Harbour, Andhra Pradesh, India, introduced (Morton 1981; also BMZD 1984219). The records from Brazil (Dunker 1853, Dall 1898, Weisbord 1964) are not accepted; see discussion below, p. 285.

Distribution. Oligocene, Panama; Miocene to Quaternary, United States and Caribbean; Late Caenozoic, Pebasian, Upper Amazon Basin. Recent, Florida, Caribbean widespread. Pacific coast of Panama, to ? northern Ecuador (possibly introduced). Presumably introduced to Panama Canal locks, India, ?West Africa, ?Fiji.

Diagnosis. *Mytilopsis* with gently curved dorsal margin; diagonal ridge well rounded; apophysis elongate, lying adjacent to dorsal margin and partly under septum.

Description. Although the outline is of variable shape, it is generally regular, showing no gross changes in relative growth rates at different parts of the mantle edge, except in the region of the byssal notch. The umbonal ridge varies in strength, but is always well rounded, not angular. The apophysis is lanceolate. It is attached to and has its long axis parallel to the dorsal margin of the shell. Its pointed, anterior, end lies against or just under the dorsal edge of the septum. Its posterior, broad, end is frequently slightly barbed. Recent examples are sometimes tinged with purple or indigo,



Figs 341–344 *Mytilopsis sallei* (Recluz). Late Oligocene, Panama; originally described as *Dreissensia dalli* Clerc *in* Joukowsky & Clerc, from Bombacho, western Panama. Joukowsky Colln, Geneva NHM, all × 3. **341**, **lectotype** (herein selected), shell figured by Clerc (*in* Joukowsky & Clerc 1906: pl. 1, figs 4, 5). a, right side; b, front view. **342**, paralectotype, same details as Fig. 341 (originally figured as pl. 1, fig. 2); left side. **343**, paralectotype, same details as Fig. 341 (originally figured as pl. 1, fig. 3); right side. **344**, paralectotype, same details as Fig. 341 (originally figured as pl. 1, fig. 1); right side.

as in the type illustration (Recluz 1852) of *M. sallei* and in BMZD specimens from Mexico (Marelli & Berrend 1978). Other Recent shells are dirty white with a yellow-brown periostracum, as shown in Reeve's (1858) illustrations of *M. sallei*, *M. rossmassleri* and *M. morchiana*. Some specimens show dark purple concentric banding, which is normally more intense on the inner shell surface.

DIMENSION. In mm.	diag l	l	h	vbr	l/h
D. sallei Recluz 1852 (from type illustration)	22.2	21.0	17.0	–	1.24
M. sallei, shell fig'd Reeve, 1858: fig. 44.	17.5	16.7	14.5	4.4	1.15
M. rossmassleri, shell fig'd Reeve: 1858, fig. 45.	19.2	17.2	16.0	4.8	1.08
BMZD 93.2.4.2048, Guatemala	19.5	15.8	17.2	3.6	0.92
BMZD 93.2.4.2049, Guatemala	24.2	21.2	15.7	4.0	1.35
LL27915, Pebasian, Canamá.	17.2	15.0	13.2	4.0	1.14
LL27966, Pebasian, Puerto Nariño.	5.2	4.1	4.0	–	1.02
PIMUZ 804, *C. fragilis* Boettger, Iquitos; de Greve 1938: pl. 9, fig. 15.	11.9	10.5	9.0	3.8	1.17
PIMUZ 820, as above, var. II, fig. 24.	33.9	28.7	27.0	–	1.06
PIMUZ 821, as above, var. II, fig. 23.	32.5	33.8	27.9	8.6	1.20
PIMUZ 826, as above, var. III, fig. 26.	37.5	38.7	27.5	8.6	1.41

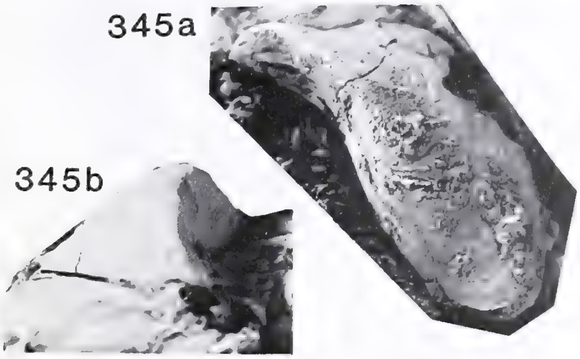
Note. The measurements of PIMUZ specimens are taken partly from de Greve's text and partly from his plates. The length measurements he gave in his text correspond to diagonal or maximum length.

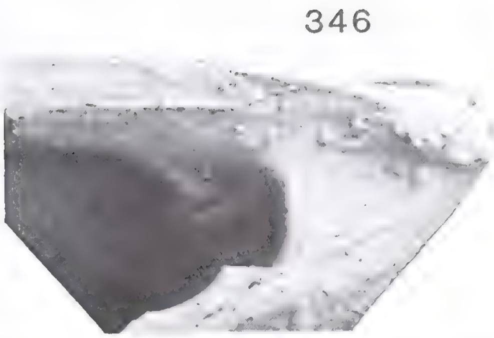
REMARKS. In the small samples of nominal species, in the BMZD collections, variation in shell outline, convexity and strength of the diagonal ridge are sufficient to encompass all the references in the above synonymy. Comparisons with *M. scripta* are given under that species (p. 287) and with *M. leucophaetus* under the genus (p. 279). The synonymy published by Marelli & Gray (1983) is accepted here except for minor points and the addition of some extra Recent references, discussed below. They did not cover fossil taxa, which are also included here.

Marelli & Gray (1983: 190–191) argue that *M. domingensis* (Recluz, 1852) is a synonym of *M. sallei*. This seems reasonable: its apophysis is of the same type and it may be regarded as being typical of the species except for its relatively elongate shell. It seems virtually impossible to tell apart the BMZD shells which Reeve figured as *M. domingensis* from the Dominican Republic, from those he figured as *M. africana* (van Beneden, 1835: 167) from Senegal (Reeve, 1858: pl. 10, fig. 47). Both lots are Cuming collection. It may be suggested that *M. africana* could have been introduced to west Africa along the old slaving routes. The decision to retain *M. sallei* as the name for the species must therefore be regarded as provisional, but any change should await the examination of freshly collected Caribbean and west African material, as there is nearly always some doubt about the accuracy of locality data with samples from old collections. Furthermore, the whereabouts of van Beneden's collection is unknown. It is not in Bruxelles NHM (A. Dhondt, personal communication).

Marelli & Gray (1983) placed *M. americanus* (Recluz) in the synonymy of *M. leucophaetus* (Conrad). I suggest that the Cuming collection shells (BMZD) are the syntypical series of *americana* (p. 282). The apophysis is of the *sallei* type. Dunker, Recluz and Reeve all appear to have made use of Cuming's collection, with the result that their interpretations of the various nominal species are likely to be in accord. Although more research would be necessary to establish whether or not Cuming samples are the syntypes of these species, Reeve's (1858) illustrations of them may still be regarded as the best available interpretation of some of Dunker's unfigured species, such as *M. morchiana*, *M. riisei* and *M. rossmassleri*. Two of Dunker's species, *M. gundlachi* and *M. pfeifferi*, both from Cuba, are unrepresented in Cuming's collection and were not figured by Reeve. Marelli & Gray (1983) placed both in the synonymy of *M. sallei*, but no opinion on them is advanced here.

The living *M. trautwineana* (Tryon, 1866*b*), from the Rio San Juan of the Pacific coast of Colombia, has a semi-straight dorsal margin and its posterodorsal slope is also straight, with these two margins meeting in a very obtuse curve. The most distinctive features of this species are probably its well rounded umbones and exceptionally large septum. It seems reasonable to suppose that this species is distinct from *M. sallei*. Clessin (*in* Miller 1879) described *M. milleri* and *M. ecuadoriana* from Esmeraldas Province, northern Ecuador.





Figs 345–346 *Mytilopsis scripta* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. **345**, LL27956; a, left valve, side; b, front view; both × 2.5. **346**, LL28100; left valve, details of interior showing septum and apophysis, × 20.

Both have been placed in the synonymy of *M. trautwineana* (Olsson 1961: 140; Keen 1971: 116).

The living *M. rossmassleri* (Dunker, 1853) was described as coming from Brazil, though Dunker had his doubts about the locality data, mentioning that the material was obtained from a trader. Both Dall (1898: 809) and Weisbord (1964) quoted its range as Florida to Brazil. Although comparatively trigonal in outline and with a straighter hinge line than usual, it cannot be considered as distinct from *M. sallei*, which is reported with confidence from Florida (Marelli & Gray 1983: 190), thus confirming that the ranges of this species and *M. leucophaetus* (Conrad) overlap. The Brazilian records of *Mytilopsis* all appear to stem from that of Dunker and are here dismissed. The nearest living occurrences are in Venezuela (Weisbord 1964; Marelli & Gray 1983). It is worth stressing that the genus is not recorded from Surinam by Vernhout (1914), nor in the very comprehensive work of Altena (1971).

The oldest known occurrence of *M. sallei* is its record from western Panama as *M. dalli* Clerc (*in* Joukowsky & Clerc 1906). Joukowsky, who collected the material and described the stratigraphy, thought that his locality was either Miocene or Pliocene. Like *M. trigalensis* Olsson, 1931 (see *M. scripta*, below), *M. dalli* occurs with an ampullinid, which Woodring (1959: 159) placed tentatively in the synonymy of *Ampullinopsis spenceri* (Cooke). Woodring also (1959: 160) mentioned Joukowsky's locality as being Late Oligocene.

The specimen figured by Maury (1917) as *M. domingensis* from the Miocene of the Dominican Republic is slightly deformed, but its almost alate posterodorsal region is typical of *M. sallei*, and thus there seems no reason to suppose that Maury's specimen is of an extinct species.

Mytilopsis scripta (Conrad, 1874) Figs 345–351

* 1874*a* *Dreissena (Mytiloides) scripta* (Conrad: 29; pl. 1, figs 12, 16.
*? 1878 *Dreissenia fragilis* Boettger: 497 (*pars*); pl. 13, figs 16a, b, 18; *non* figs 17a–c.
*v 1879 *Dreissena acuta* Etheridge: 82; pl. 7, fig. 1.
. 1897 *Congeria fragilis* (Boettger) Andrussov: 141 (Russian text); 30 (German text).
*. 1898 *Congeria lamellata* Dall: 809 (*pars*).
. 1924 *Dreissena acuta* Etheridge; Roxo: 44 (*pars*); Figs A3, A′3, A4, A′4; *non* figs A1, A′1, A2, A′2.
*v 1931 *Mytilopsis trigalensis* Olsson: 42 (138); pl. 1 (13), figs 3, 8, 9.
*. 1935 *Mytilopsis cira* Pilsbry & Olsson: 19; pl. 5, fig. 2.
. 1938 *Congeria scripta* (Conrad) de Greve: 56; pl. 9, figs 4, 5, 10, 12; text-figs 4, 5.
. 1938 *Congeria fragilis* (Boettger); de Greve: 49 (*pars*); pl. 9, figs 8, 9, 14; *non* fig. 15.
. 1938 *Congeria* cf. *fragilis* (Boettger) de Greve: 51; pl. 9, figs 19, 20.
. 1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. I de Greve: 53; pl. 9, figs 13, 16, 17.
. 1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. IV de Greve: 55; pl. 9, figs 18, 21, 22.
. 1944 *Mytilopsis scripta* (Conrad) Pilsbry: 152.
. 1968 *Mytilopsis scripta* (Conrad) Richards: 83.

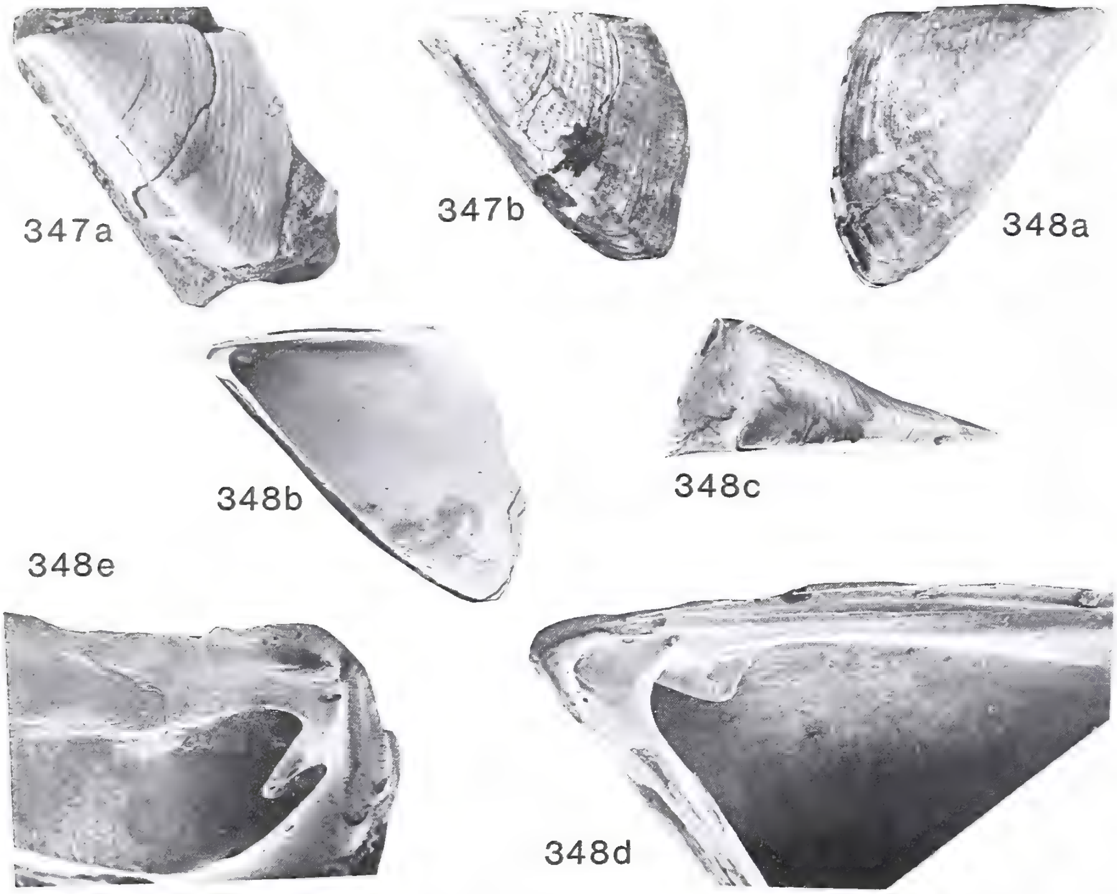
TYPE MATERIAL. Types of *Mytilopsis scripta* Conrad not studied. Conrad (1874*a*) figured several syntypes, one fully grown shell (pl. 1, fig. 16) and three juveniles (pl. 1, fig. 12). His specimens came from either Pebas, Old Pebas or Pichana. Pilsbry (1944) wrote of revealing the myophore on the underside of the septum when cleaning Conrad's type specimen. Richards (1968: 83) listed a possible paratype as being in ANSP (not registered).

Holotype of *Dreissena acuta* Etheridge, BMPD LL27913, Late Caenozoic; Canamá (C. Barrington Brown colln). Etheridge (1879) stated that he had only the one figured specimen, and in view of this the two others found with it cannot be regarded as paratypes. One, LL27914, is this species; the other, LL27915, is now identified as *M. sallei* (Recluz); see p. 283.

Holotype of *Mytilopsis trigalensis* Olsson (1931 : pl. 1, fig. 3; PRI 1927) and paratype (1931: pl. 1, fig. 8; PRI 1932), both ? Late Oligocene, Quebrada Boca Pan, western Peru.

OTHER MATERIAL STUDIED. All late Caenozoic. BMPD LL27911–2, LL27956, LL28100–4, Pebasian; Pichana, Peru (Hauxwell Colln, 1870), extracted from matrix, 1981); LL27901–2, Loc. 33, 570–670 cm, La Tagua, Colombia (Eden Colln); LL28120–9, as *Congeria lamellata* Dall, Caloosahatchee Formation; Florida (Sowerby & Fulton Colln, 1899) (Figs 352–354).

FURTHER RECORDS. Type locality of *Mytilopsis cira* Pilsbry & Olsson (1935), originally given as either late Oligocene or early Miocene, but redated as ? Miocene herein. La Cira Formation, Rio Oponcito area, near Guanabanas, Magdalena Valley, Colombia (fairly common; Pilsbry & Olsson 1935); Late Caenozoic, Pebasian: Pebas (Boettger 1878); Iquitos (de Greve 1938); Três Unidos (Roxo 1924).



Figs 347–348 *Mytilopsis scripta* (Conrad). Pebasian; Canamá, Peru; originally described as *Dreissena acuta* Etheridge; Barrington Brown Colln. **347**, LL27913 (*ex* BMPD 97730); holotype of *Dreissena acuta* Etheridge, figured by Etheridge (1879: pl. 7, fig. 1); a, b, left valve, × 3. **348**, LL27914; right valve found with LL27913, but not mentioned by Etheridge; a, side view, × 5; b, front view, × 8; c, interior, × 5; d, interior, detail showing septum and apophysis, × 20; e, umbonal region viewed from posterior end of shell showing apophysis hanging below dorsal margin of septum, × 20.

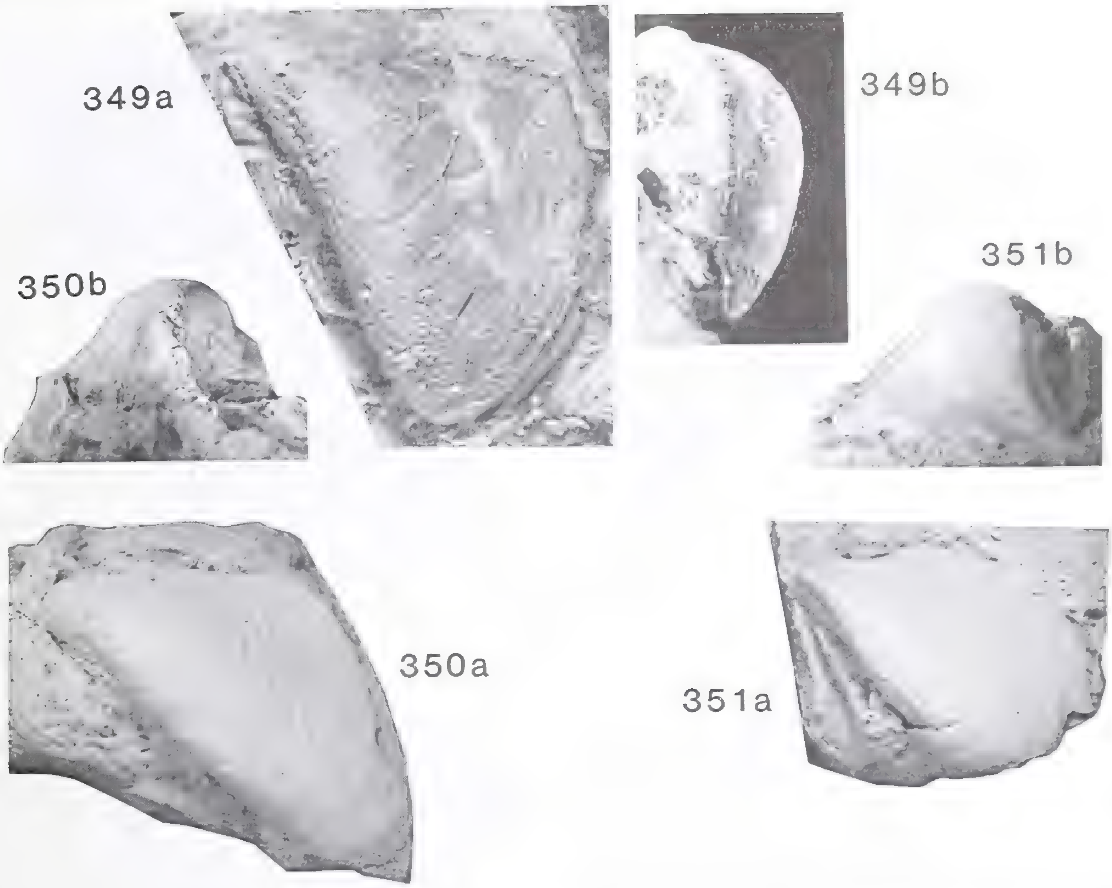
DISTRIBUTION. Late Oligocene, western Peru; ?Miocene, Magdalena Valley, Colombia; Late Caenozoic, La Tagua; Late Caenozoic, Pebasian (Pebas, Pichana, Iquitos, Canamá, Três Unidos).

DIAGNOSIS. *Mytilopsis* with a straight dorsal margin and prominent umbonal ridge; shell outline often markedly trigonal, but sometimes less regular; apophysis similar to that of *M. sallei*, relatively lanceolate, adjacent and parallel to dorsal margin of shell. Colour patterning variable, but sometimes prominent.

DESCRIPTION. The dorsal margin is almost straight and is usually about two-thirds of the total shell length, though sometimes, as in the case of Conrad's type illustration (1874*a*: pl. 1, fig. 16), it is much shorter. The outline is rather variable. At one extreme there are specimens such as LL27956, rather similar to Conrad's type illustration; at the other, the shell is much more triangular as in the holotype of *D. acuta* Etheridge, the type illustration of *M. cira* Pilsbry & Olsson and the two La Tagua specimens. Intermediate stages occur. Examples from Iquitos covering the whole range of variation are illustrated by de Greve (1938: pl. 9). The umbonal angle is also variable. In anterior view, the posterodorsal and anteroventral slopes meet at about right angles to form a prominent umbonal ridge. The ridge itself is sometimes well rounded but often angular. The byssal gape is not easily seen. The septum and apophysis can be seen in LL27914 from Canamá and in several juveniles (e.g. LL27912) from Pichana. Unfortunately, neither the muscle scars nor pallial line are visible enough to be described. The shell is thin. Colour patterning may be seen on some specimens and is variable, consisting either of concentric rays, or of broad zigzag bands, or of radiating patterns of lines or blotches.

DIMENSIONS. In mm.	diag. l	l	h	vbr	l/h
Conrad's type illustration 1874*a*: pl. 1, fig. 16): proportions only, no scale given.	22	17	17	–	1
LL27956, Pichana.	20.8	16.0	18.4	–	0.87
LL27902, Loc. 33/570–670, La Tagua.	7.2	6.1	6.0	–	1.02
LL27913, holotype of *D. acuta* Etheridge, Canamá.	14.3	10.7	10.6	–	1.01
LL27914, *D. acuta* Etheridge, Canamá.	9.6	6.8	7.4	1.8	0.92
M. cira, from Pilsbry & Olsson, 1935: 19.	16.75	–	14	4.25	–
M. cira, from Pilsbry & Olsson, 1935: 19.	18.25	–	16.5	6.25	–

Note. Pilsbry & Olsson (1935) did not indicate which of their measured specimens was the type and gave no scale for their type illustration.



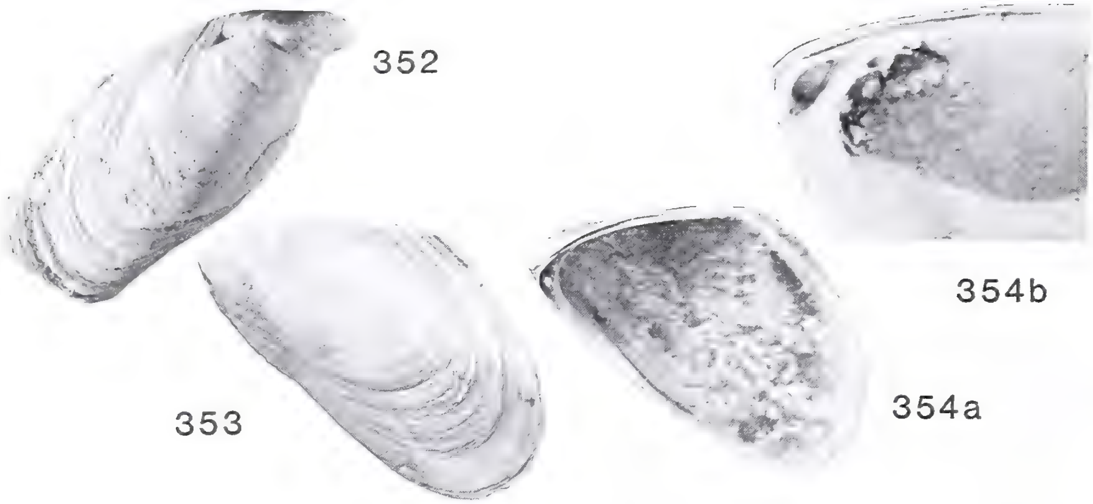
Figs 349–351 *Mytilopsis scripta* (Conrad). Late Caenozoic; La Tagua, and from Pacific coastal area of Peru (originally described as *M. trigalensis* Olsson). **349**, *Mytilopsis scripta* (Conrad), LL27902; Late Caenozoic; La Tagua, Loc. 33/570–670; Eden Colln. a, left valve, side, × 8; b, elevation of anteroventral side. × 5. **350**, PRI 1927; holotype of *Mytilopsis trigalensis* Olsson, figured by Olsson (1931: pl. 1, fig. 3); Late Oligocene; Quebrada Boca Pan, western Peru. a, left valve, side; b, anterior; both × 3. **351**, PRI 1932; paratype of *M. trigalensis*, same details as holotype, originally figured by Olsson (1931: pl. 1, fig. 8). a, left valve, side; b, anterior; both × 3.

REMARKS, *M. scripta* may be easily distinguished from other species of *Mytilopsis* by the straightness of its dorsal margin, coupled with the angularity of its diagonal umbonal ridge. The dorsal margin of *M. leucophaetus* (and its probable synonym, *M. jamaicensis* Woodring, 1925) may be straight, but its umbonal ridge is not so prominent and its apophysis is different from those of both *M. sallei* and *M. scripta*. In *M. sallei*, the dorsal margin is curved to some extent and it merges fairly gradually, with less of an angulation, with the posterior margin of the shell. In *M. scripta*, however, the straight dorsal side and the high, angular, diagonal ridge are strongly reminiscent of the living European *Dreissena polymorpha* (Pallas). Some Recent samples in BMZD, previously identified as *M. rossmassleri* (Dunker) which is now synonymized with *M. sallei*, have comparatively straight hinge lines and strong posterior angulations, but they lack the prominent umbonal ridge of *M. scripta*. In contrast, *M. trigalensis* Olsson (1931) from the Oligocene of Peru resembles *M. rossmassleri* in outline, but is here placed in *M. scripta* because it is strongly ridged. *M. trigalensis* also has some resemblance to the living Pacific drainage species *M. trautwineana* (Tryon), but the latter may be distinguished by its blunter beak and weaker umbonal ridge. Unfortunately, the internal characters of *M. trigalensis*, preserved in hard limestone, are unknown, so no comparison is possible with the unusually large septum of *M. trautwineana*.

Conrad (1874*a*) referred to the colour patterning of zigzag brown lines on his specimens. Similar markings are also present on an Iquitos shell (de Greve, 1938: pl. 9, fig. 12). A few BMPD shells from both Pichana and Canamá show such markings, whilst the colour patterning on a La Tagua specimen (LL27901) consists only of concentric bands. It would thus appear that although such clear-cut colour patterning has not been seen in living species of *Mytilopsis*, it is not an essential feature of *M. scripta*.

When describing *D. fragilis* from Pebas, Boettger (1878) was clearly unaware of Conrad's earlier description of *D. scripta*. The identity of Boettger's species is uncertain. He figured three specimens (1878: pl. 13, figs 16–18). Only fig. 17 was sufficiently complete to be recognizable, and as its hinge line is moderately curved, it is assigned with some confidence to *M. sallei* (Recluz). His fig. 16 lacks the hinge line, whilst his fig. 18 could be either a dorsal or ventral view of a bivalved specimen lacking the umbones. De Greve (1938: 50; pl. 9, fig. 9) figured a shell which he referred to as the original of Boettger's 'pl. 14' (*sic*), fig. 18. De Greve's figure is of a left valve, including the umbo, of a specimen exhibiting the straight hinge line of *M. scripta*: it is certainly not one of Boettger's figured syntypes.

The characters used by de Greve (1938) to separate *M. fragilis* (Boettger) from his 'cf. *fragilis*' and the 'varieties I to IV' of his 'nov. sp. aff. *fragilis*' appear from his illustrations to



Figs 352–354 *Mytilopsis lamellata* (Dall). Plio-Pleistocene, Florida. **352**, LL28109; specimen referred herein to *M. sallei* (Recluz), with *M. sallei*-type apophysis and with external shape resembling its junior synonym, *M. domingensis* (Recluz). Sowerby & Fulton Colln. Right valve, × 2.5. **353**, LL28120/1; specimen herein referred to *M. leucophaetus* (Conrad), same sample as Fig. 352; left valve exterior, × 2.5. **354**, LL28120/2; specimen herein referred to *M. leucophaetus* (Conrad); same sample as Fig. 352. Right valve interior, a × 2.5, b × 10.

be inconsistent. In the present paper, those with straight hinge lines are placed in *M. scripta*, whilst the remainder seem to fall within the range of variation encountered in living *M. sallei*.

The figure of the holotype of *M. cira* Pilsbry & Olsson (1935) shows that its posterodorsal region is damaged, but earlier growth lines indicate that it was correctly described as having a straight dorsal margin. This specimen has a rather trigonal outline and a sharply angled umbonal ridge. Pilsbry & Olsson did not compare their species with any other, but it clearly seems to be synonymous with *M. scripta*.

M. trigalensis Olsson (1931) was omitted by Weisbord (1964: 206–211) from his list of western hemisphere *Mytilopsis*. It was described from the small fauna of the Punta Brava Grits of the Mancora Formation of the Pacific coastal region of northern Peru. Both the Mancora and the overlying Heath Formation were thought by Olsson to be Oligocene. In his account of the stratigraphy (1931: 12), he seemed sure that the Trigal locality underlay the Heath Formation. Eames (*in* Morley Davies 1973: 296), however, suggested that the Mancora Formation was early Miocene on the grounds that it contained *Ampullinopsis spenceri* (Cooke) and also was believed to be the equivalent of horizons in southern Peru and southern Ecuador containing the age-diagnostic benthonic foraminifera *Miogypsina gunteri* and *Miolepidocyclina ecuadoriensis*. Eames gave neither names nor localities for these horizons and offered no supporting evidence for his correlation. Bristow (1975: 128–129), writing without knowledge of Eames' work, quoted the views of other workers who supported an Oligocene dating. *Ampullinopsis spenceri* (Cooke) also occurs at the Panamanian type locality of *Mytilopsis dalli* Clerc, *in* Joukowsky & Clerc, but Olsson's determination of this species was not accepted as definite in the synonymy of that species given by Woodring (1959: 159). Thus, on present evidence, there seem to be no compelling reason for rejecting an Oligocene age for *M. trigalensis*, which along with *M. dalli* (placed here in *M. sallei*) are probably the oldest *Mytilopsis* in the western hemisphere.

Order **MYOIDA** Stoliczka, 1870
Superfamily **MYACEA** Lamarck, 1809

[*nom. transl.* Gill (1871: 18), *ex* Myaires Lamarck (1809: 319; 1818: 423, 459); Myacea (family) Goldfuss (1820: 613)]

Family **CORBULIDAE** Lamarck, 1818

[*nom. correct.* Gray (1840: 150) *ex* Corbulidées Lamarck (1818: 423, 493); Corbuladae Fleming (1828: 425)]

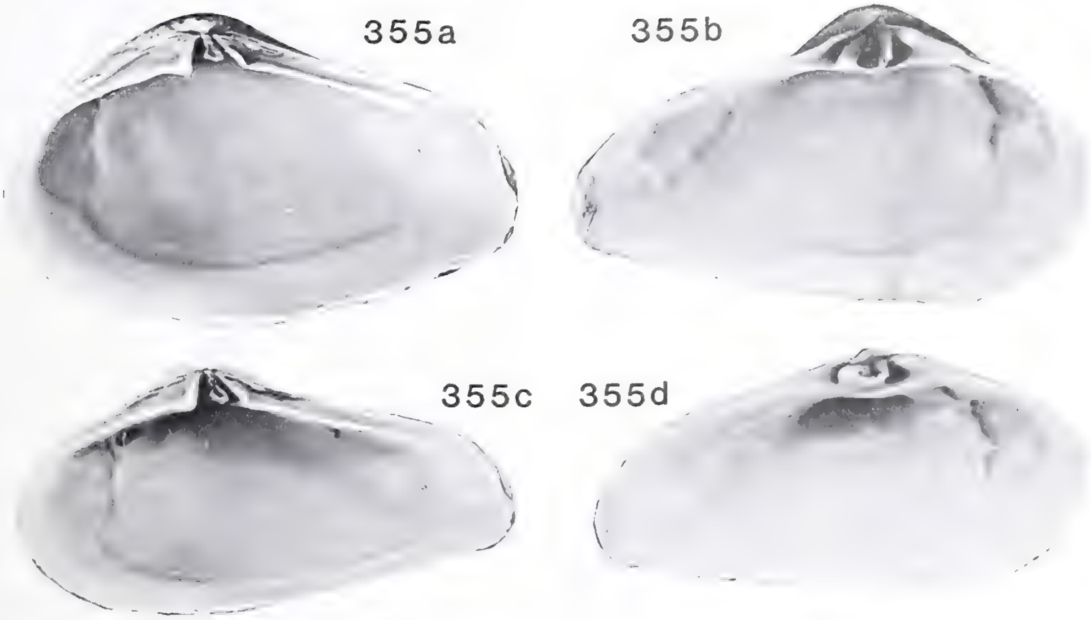
Subfamily **PACHYDONTINAE** Vokes, 1945

[Pachydontinae Vokes (1945: 6)]

Keen *in* Moore (1969: N692) credited Broderip, (1839) with latinizing 'Corbulidées' Lamarck as Corbulidae. I have been unable to trace this reference: the earliest use of the family name Corbulidae I have been able to find is that by Gray (1840).

Vokes (1945), in his revision of the Corbulidae, proposed what he described as a tentative new classification, with the erection of several new subfamilies, including the Pachydontinae. In this he placed only two genera, *Pachydon* Gabb, 1869, from the late Tertiary of the Upper Amazon Basin and *Tiza* de Gregorio, 1890, from the Vicksburg Oligocene of Mississippi.

In the present paper, it is suggested that *Tiza* is unlikely to be closely related to *Pachydon* and should therefore be removed from the Pachydontinae. Three other genera, *Pebasia* gen. nov. (p. 315) and *Ostomya* Conrad (1874*a*), both occurring in the same deposits as *Pachydon*, and the living *Guianadesma* Morrison (1943) from the Guyanas, are now assigned to the Pachydontinae. Most previous authors have considered *Guianadesma* to be a junior synonym of *Ostomya*, usually placed in the Lyonsiidae. Most of the reasons for proposing these chages in the classification are given below,



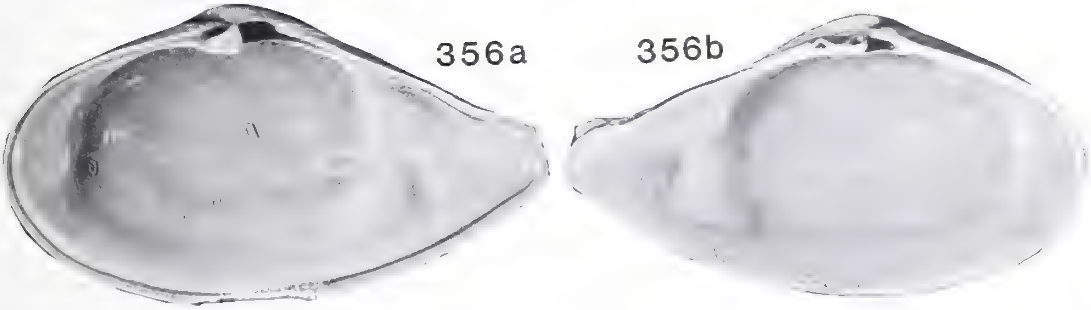


Fig. 355 *Erodona mactroides* (Bosc). BMZD 1854.12.4.754; Recent; specimen identified by d'Orbigny as *Azara labiata* (Maton) from sample labelled 'Buenos Aires and Montevideo'; d'Orbigny colln. a–d, left and right valve internal, normal and slightly tilted views, × 3.

Fig. 356 *Corbula (Caryocorbula) ovulata* Sowerby. BMZD 1984227; Recent; Pacific Coast of Mexico; Cuming Colln. a, b, left and right internal views, × 3.

though a few points are more appropriately dealt with in the remarks following the diagnosis of a particular genus.

Vokes (1945: 6), whose study was based mainly on type species of genera, defined the Pachydontinae as follows: 'Valves tending to be distorted, with the ligamental area so twisted that the resilium was attached to the lateral, rather than to the dorsal face of the condrophore.' Other features of *Pachydon* which should be taken into account in recognizing the subfamily are that the shell is almost smooth and that there are no abrupt changes in post-neanic shell characters as in many other members of the Corbulidae (Cox *in* Moore 1969: N100, fig. 83). The right cardinal tooth is unusual in that in many species its anterior surface is visible from the outside. In species with very incurved umbones, including the type species *Pachydon obliquus* Gabb, this tooth is not in contact with the outside world, but a small lunule-like swelling is present. The hinge plate anterior to the cardinal tooth is either reduced or lacking in the subfamily. Recent *Corbula* and *Erodona* are illustrated for comparison with *Pachydon* (Figs 355–356).

I have not examined specimens of *Tiza*, but Vokes' illustrations (1945: pl. 4, figs 16–22) show that the right cardinal tooth is not close to the outside world and that a substantial area of anterior hinge plate exists. Although *Tiza*, like *Pachydon*, is comparatively smooth and its commissure is twisted, it appears unlikely that the two genera are closely related. It seems much more plausible that *Pachydon* developed independently in the non-marine environment widespread in the Tertiary of northern South America.

Vokes (1945: 27), in a section on names he was rejecting from the Corbulidae, dealt with *Ostomya*, which Conrad (1874*a*) had described from the Pebasian deposits. Vokes placed in its synonymy the living South American *Himella* H. Adams, 1860 (*non* Dallas, 1852, Hemiptera), *Anticorbula* Dall, 1898 – which had been proposed as a replacement name for *Himella* Adams – and *Guianadesma* Morrison, 1943. These genera are each monotypic. Adams described his species *Himella fluviatilis* as a member of the Corbulidae and wrote that it came from the River Marañón. Conrad thought that his *Ostomya papyria* was a member of the Anatinidae (now Laternulidae). Morrison collected his new genus and species *Guianadesma sinuosum* live in Guiana. He interpreted it as an aberrant member of the Lyonsiidae which had lost its ligamental ossification. Vokes' synonymy is the same as that given by Pilsbry (1944), with whom he had been in correspondence on the matter. Pilsbry, however, accepted *Ostomya* as a member of the Corbulidae whilst Vokes, in rejecting it as such, thought that it was probably a member of the Lyonsiidae as suggested by Morrison. Keen *in* Moore (1969: N847) has also followed the same synonymy and placed *Ostomya* in the Lyonsiidae, but her diagnosis, perforce following that of Conrad (1874*a*), has the hinge structures of the two valves transposed.

In the present paper *Himella fluviatilis* is regarded as a *nomen dubium*. The types of both *Himella fluviatilis*, which Adams did not figure, and of *Ostomya papyria* are lost. The material upon which Adams based his description of *H. fluviatilis* was in the Cuming Collection and had been obtained from the naturalist Bates who collected from both the Guianas and the Amazon Region. There is no trace either of these specimens or of any other material bearing this name in BMZD. All subsequent authors' opinions about these two genera have been based on Conrad's rather poor figure and on specimens in ANSP identified as *Himella fluviatilis* and eventually figured by Pilsbry (1944). Pilsbry, however, does not explain how they came to be so identified and no connection with Adams' type material can be found. These specimens are clearly conspecific with *Guianadesma sinuosum* Morrison. Because of the complete lack of authenticated material neither the genus *Anticorbula* Dall not the species *fluviatilis* H. Adams can be defined except by reference to the type series of *Guianadesma sinuosum* Morrison. I have therefore decided to use the name *Guianadesma sinuosum* Morrison here rather than to follow either Altena (1971: 82), who referred to *Anticorbula sinuosum*, or Pilsbry (1944), who used *Ostomya fluviatilis* Adams; both the latter are regarded here as *nomina dubia*. Confidence in ever establishing the true identity of *Anticorbula fluviatilis* is further undermined by doubts about the locality data. Both Adams' and Pilsbry's shells were said to come from the River Marañón. There is a strong probability that Pilsbry's were mislocalized for, as has been said, they clearly belong to *G. sinuosum*, a species so far known living only in the Guianas. If Adams was correct in stating that his species came from the fresh-water Marañón, it might be expected that it would be distinct from the brackish-water *G. sinuosum*, living 2000 km further to the east.

The type locality of *Ostomya papyria* could be any one of the three fossil localities visited by Steere (*in* Conrad, 1874*a*: 26–27), Pebas, Old Pebas or Pichana. These lie within 25 km of each other and have yielded very similar faunas. They are thought to be of the same geological deposit and are certainly of very similar age and facies. Newly extracted specimens from the matrix of Hauxwell's collection from Pichana are almost certainly of *O. papyria*, and are indeed from one of the possible type localities. They resemble Conrad's figure closely and cannot easily be confused with other known species in the fauna. They also agree with the original description, bearing in mind that Conrad also confused the left and right valves of two other species of bivalves he described in the same paper, *Pachydon* (*Anisorhyncus* ?) *dispar* – now the type species of *Pebasia* – and *P. (A.) cuneiformis* (1874*a*: 26, 27). Pilsbry (1944: 147–149) clearly did not have Conrad's material for study when discussing *Ostomya*, though in the same paper (1944: 149–150) he went on to redescribe *Pachytoma tertiana* and *Tropidobora eborea*, both of which were also originally described by Conrad (1874*a*). These were both listed by Richards (1968), who does not record *O. papyria*.

The hinge structures of *Ostomya* and *Pachydon* show strong similarities; that of *Guianadesma* is one of the same general type, but is reduced. A feature common to all three is the lanceolate resilifers disposed in different planes in the two valves, and the twisting of the ventral commissures. The shells of the Lyonsiidae are always predominantly nacreous (Taylor *et al.* 1969, 1973, Prezant 1981). Morrison (1943: 50) described the shell of *Guianadesma* as nacreous-porcellanous within. I have examined under the binocular microscope (at ×30 and ×100) all the available material of *Guianadesma*, *Ostomya* and *Pebasia*, along with numerous specimens of *Pachydon* and both Recent and fossil *Corbula*, including the rather porcellanous *Bicorbula gallica* (Lamarck) from the Eocene of France. The shell of all of these appears to be very similar, consisting of crossed lamellar and complex crossed lamellar structure. Nacre has not been observed.

Morrison (1943) also described the inner and outer branchiae of *Guianadesma* as subequal and (1943: 50) as eulamellibranchiate. He gave no indication that the branchiae were distinctively unusual as in *Lyonsia* and *Pandora* (Ridewood 1903: 151–152, text-figs 1B, 2J; Cox *in* Moore 1969: N20, fig. 20). In fact, Morrison did not base his reasons for placing *Guianadesma* in the Lyonsiidae on either shell structure or gill type.

It is clear that neither *Ostomya*, *Guianadesma* nor *Pebasia* belong to the Lyonsiidae and the features they share with *Pachydon* are sufficient grounds for placing them all in the Pachydontinae. The possibility remains, however, that *Guianadesma* and *Ostomya* may be descended from some other corbulid ancestor which independently invaded brackish and possibly fresh water environments in South America during the Tertiary. So far, *Ostomya* is known only by its type species *O. papyria* Conrad. All other records of that genus are here rejected, some being of *Guianadesma*. The presumed earliest record of *Guianadesma* is *G. colombiana* (Pilsbry & Olsson, 1935) – originally described as *Ostomya* – from the ? Late Oligocene or early Miocene La Cira Formation, in which *Pachydon cebada* (Anderson) also occurs. It seems possible that these genera both originated at about the same time. *Guianadesma* is of special interest as the sole surviving possible member of the Pachydontinae.

Genus ***PACHYDON*** Gabb, 1869

[= *Anisothyris* Conrad (1871*b*: 196), an unjustified substitute name for *Pachydon*; = *Pachydon* (*Anisorhynchus*) Conrad (1874*a*: 28; type species by monotypy *Pachydon* (*Anisorhynchus*) *cuneiformis* Conrad 1874a: 28), Late Caenozoic, Pebasian; Peru.]

TYPE SPECIES. *Pachydon obliquus* Gabb, 1869, by subsequent designation of Dall (1872: 91) and independently by Meek (1876: 240). Late Caenozoic; Pebas, Peru.

DIAGNOSIS. Small to large Pachydontinae, up to 50 mm in length; surface often almost porcellanous, with weak growth lines; weak concentric ribbing mainly on later growth stages and posterior slope; umbones often strongly incurved and prosogyrous; sometimes equivalve but normally with right valve more convex than left; commissure often markedly twisted; right valve margin often grooved for reception of left valve with posterodorsal portion of groove sometimes developing into elongate posterolateral socket; right cardinal tooth massive and adjacent to outside world in most species; lunule-like protuberence often present in front of umbones; right posterior resilium pit trigonal and deep, arising at umbo and sloping in a posteroventral direction, thus partly obscured by cardinal tooth; resilifer lanceolate and forming shallow groove slightly posterior to the centre of the socket; left valve with deep trigonal cardinal socket, separated by weak postero-

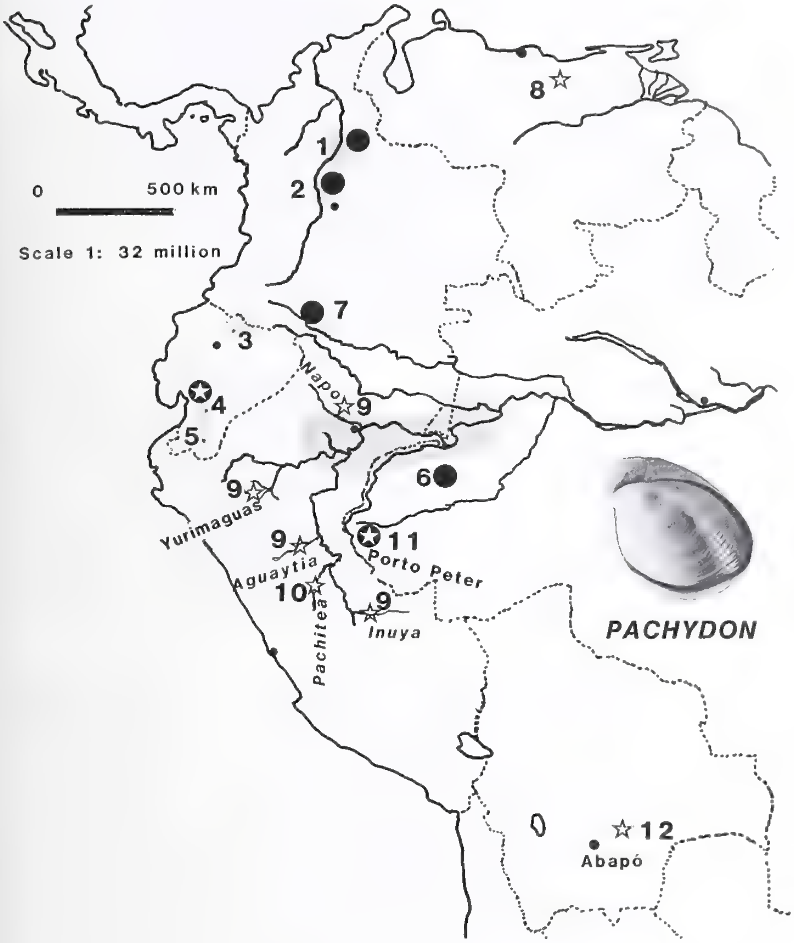


Fig. 357 Neogene distribution of the extinct genus *Pachydon*. Key as for Fig. 6 (p. 177) with additions: 8, Venezuela (Rutsch 1951); 9, Peruvian localities of Bassler (Willard 1966); 10, Pachitea River as *Corbula arcana* (Pilsbry 1944); 11, Porto Peter, Brazil as *Anisothyris acreana* (Maury 1937); 12, Taterenda Formation, Bolivia, as *Tellina* sp. (Mather 1922). Inset: *P. obliquus* Gabb, Pichana. × 1.5. Black circles, = authenticated records; white stars, = doubtful records; white stars in black circles, = discredited records.

dorsal septum from overlying resilifer; resilifer lanceolate, lying almost in plane of commissure and subparallel to hinge, bordered dorsally by elongate process which functions as posterolateral tooth; mantle cavity rather small, with pallial line some distance from commissure; pallial sinus very shallow, normally only a truncation of the pallial line in front of posterior adductor scar; anterior and posterior pedal or byssal muscle scars situated at dorsal margins of anterior and posterior adductor scars respectively; other scars situated either just above the first anterior pedal (or byssal) or on anteroventral surface of hinge plate and also under hinge plate. Shell structure, outer layer crossed lamellar; inner layer within pallial line, complex crossed lamellar.

Other species assigned. *Pachydon tenuis* Gabb, 1869 (= *Pachydon ovata* Conrad, 1871*b*, = *Anisothyris hauxwelli* Woodward, 1871, unjustified replacement name for *P. tenua* Gabb); *Tellina amazonensis* Gabb, 1869; *Pachydon carinatus* Conrad, 1871*b*; *Pachydon erectus* Conrad, 1871*b* (= *Pachydon alta* Conrad, 1871*b*, = *Corbula canamaensis* Etheridge, 1879); *Anisothyris erecta elongata* Boettger, 1878; *Pachydon cuneatus* Conrad, 1871*b* (= *Anisothyris tumida* Etheridge, 1879); *Corbula* (*Anisothyris?*) *ledaeformis* Dall, 1872; *Corbula hettneri* Anderson, 1928; *Corbula cebada* Anderson, 1928 (= *Corbula abundans* Pilsbry & Olsson, 1935, = *Corbula magdalensis* Pilsbry & Olsson, 1935); *Anisothyris iquitensis* de Greve, 1938; *Pachydon trigonalis* sp. nov. (p. 309); *Pachydon ovalis* sp. nov. (p. 305).

Doubtful species. *Anisothyris acreana* Maury (1937: 4), Late Caenozoic; Valley of Rio Juruá, Acre Province, Brazil. This species is based on internal moulds and the type illustrations (1937: figs 1–4) show no characters diagnostic of *Pachydon*. The age of the type locality was reviewed by Simpson (1961), who concluded that it was probably Pleistocene, if not younger, and quoted the opinion of D. W. Taylor that the species might belong to the Corbiculacea. Both *?Ostomya terminalis* Pilsbry, 1944 and *?Corbula arcana* Pilsbry, 1944 were described from the Pachitea River Red Beds of imprecisely known Tertiary age. Neither species is generically determinable from their type illustrations. None of these doubtful species have been examined in the course of the present study.

Distribution. Unknown living. Widespread during the late Caenozoic of northern South America, particularly in Pebasian deposits of the Upper Amazon Valley of easternmost Peru and adjoining regions of Colombia and Brazil. Now also recognized in the following deposits, all thought to be Miocene: La Tagua Beds, Caqueta River, Colombia; La Cira Beds, Middle Magdalena Valley, Colombia; Santa Teresa Formation (*ex* Guaduas Beds of Anderson, 1928), Upper Magdalena Valley, Colombia. Recorded from ill-defined horizons and localities in Venezuela (Rutsch 1952). The genus is unknown in Ecuador (Cuenca Basin, etc.); the record of *Erodona iquitensis* (de Greve, 1938) in Bristow & Parodiz (1982:31) appears to be based on a misidentified specimen, BMPD LL27817, of *Corbicula cojitamboensis* Palmer, *in* Liddle & Palmer 1941. See p. 315.

REMARKS. The distribution of this genus provides some of the most important palaeontological evidence on the Neogene palaeogeography of northern South America, and is discussed in more detail in a later section, especially p. 353.

The first designation of a type species, *Pachydon obliqua* Gabb, by Dall (1872 : 91) has been generally overlooked: fortunately the later, but usually accepted, designation by Meek (1876: 240) was of the same species, which also has the merit of being common.

Vokes (1945) was correct in retaining Gabb's original name *Pachydon*. He pointed out that although *Pachyodon*, first used by von Meyer, 1838, for a mammal, is a valid name, this was no reason for adopting, as most authors have, Conrad's substitute name *Anisothyris*. Conrad's own usage was peculiar: in spite of the fact that he proposed this unjustified substitute name, he always described (1871*b*, 1874*a*) the numerous species he dealt with under *Pachydon*.

The lengthy diagnosis and discussion given here is warranted by the wide variation in morphology exhibited by the genus and the fact that Vokes' views were based largely on his study of the type species only, which happens to be one of the most inequivalve so far discovered. In sorting over 1000 specimens from Pichana in the Hauxwell Collection (BMPD), it became clear that six apparently sound species occurred together. Most of the specimens were individual shells, but the presence of several blocks provided some confirmation of co-occurrence. Individual specimens may be assigned to species with confidence and shells showing characters intermediate between species have not been found. Material from other localities supports this view. The collection from Pichana is dominated by large numbers of *P. obliquus* Gabb and *P. tenuis* Gabb; most of the other species are comparatively rare.

Dall (1872) argued at some length that there were no hard and fast reasons for separating *Pachydon* – for which he used the name *Anisothyris* – from *Corbula*, but finally concluded that subgeneric separation was desirable. He wrote (1872: 91) that 'there is a general physiognomy which is somewhat peculiar, though valueless when subjected to rigid criticism; and the following characters are especially emphasized in most of the species. The beaks are usually (but not always) more oblique and more posterior and more spiral than in most *Corbula*, and the external surface is usually smoother, though often like that of typical *Corbula* . . .' His views must still command some support. Within the genus, the wide variation in shell shape, which is possibly due to different species adopting different attitudes within the substrate, may be linked with differences in the hinge regions. Thus the shapes and attitudes and positioning of the right cardinal tooth, of the various sockets, resilium pits and resilifers, of the umbones and the adductor muscles, and also the presence or absence of lateral teeth have all varied in order that the two valves might articulate correctly. The genus includes the highly gibbous *P. erectus* Conrad, with a truncated anterior and rather alate posterior, and the slim *Paphia*-shaped *P. amazonensis* Gabb: both of these are virtually equivalve. There are also several moderately inequivalve species, such as *P. tenuis* Gabb, and the very inequivalve *P. obliquus* Gabb, with cornuate umbones reminiscent of *Glossus*. Examination of the very large number of specimens available suggests that there is no justification in erecting separate genera for equivalve and inequivalve species. *Pachydon*, therefore, must be recognised on a variety of features which are not constant for all species but, taken together, are unusual for the Corbulidae, and provide justification for Vokes' Subfamily Pachydontinae.

The first valid use of *Anisorhynchus* was by Schönherr (1842) for Coleoptera. *Anisorhynchus* Conrad (1874*a*: 28) was described as a subgenus of *Pachydon*, but is here regarded as being synonymous. It was based on what Conrad described as a single right valve – now lost – of its type species, *P.* (*A.*) *cuneiformis* Conrad (1874*a*: 28), but his inadequate figure (pl. 1, fig. 19) is of a left valve. It appears to be a typical *Pachydon*: no dimensions were given. On the previous page (1874*a*: 27) Conrad described another, very different species, as *P.* (*Anisorhynchus* ?) *dispar*, again confusing the two valves. This is here made type species of the new genus *Pebasia*. Other molluscan usages of *Anisorhynchus* were reviewed by Vokes (1945: 15, 16) under his substitute name *Ursivirus* for a very different Cretaceous taxon.

The name *Pachydon*, meaning 'thick tooth', is derived from the Greek word οδούς, a tooth, which is masculine. Trivial names which are adjectives have been inflected to agree where necessary.

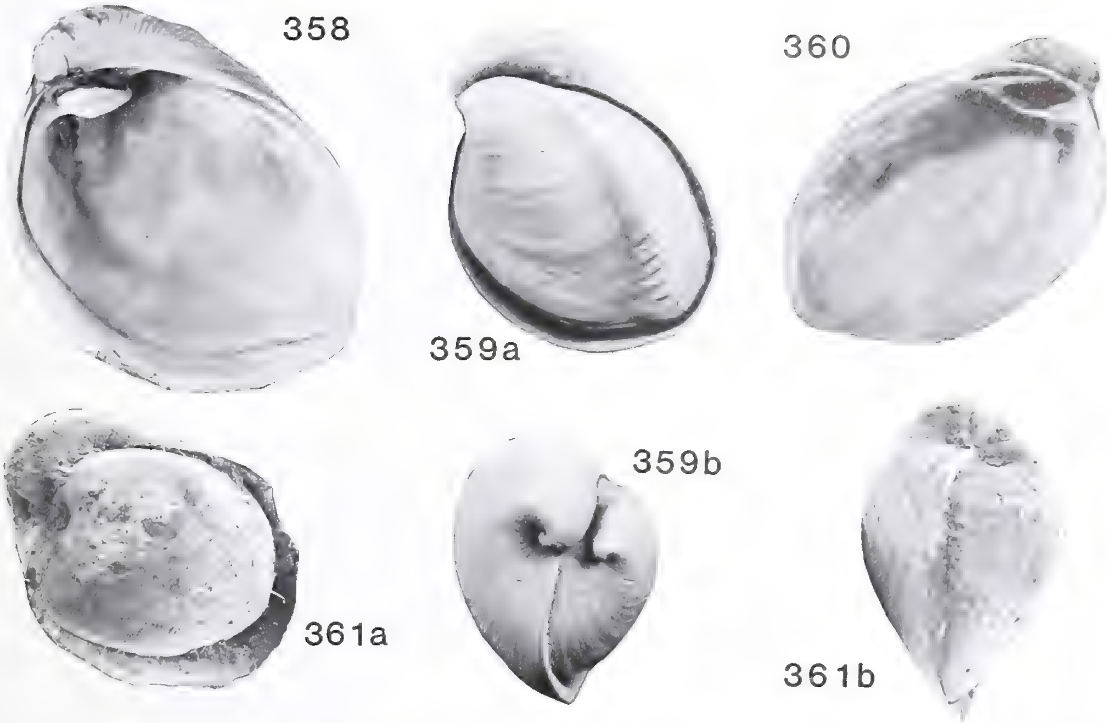
Pachydon obliquus Gabb, 1869 Figs 358–361

* 1869 *Pachydon obliqua* Gabb: 99; pl. 16, figs 5a–e.
. 1871*b* *Pachydon obliquis* Gabb (*sic*); Conrad: 196; pl. 10, fig. 15.
v. 1871 *Anisothyris (Pachydon) obliqua* (Gabb) Woodward: 106; pl. 5, figs 5a, b.
. 1872 *Corbula (Anisothyris) obliqua* (Gabb) Dall: 91.
. 1878 *Anisothyris obliqua* (Gabb); Boettger: 501; pl. 14, figs 18–22.
. 1878 *Anisothyris obliqua* (Gabb)–*A. carinata* (Conrad), transitional form; Boettger: 501; pl. 14, figs 16, 17.
. 1887 *Corbula (Anisothyris) obliqua* (Gabb); Fischer: 1124.
. 1906 *Pachydon obliquus* Gabb; Clarke: 133.
. 1938 *Anisothyris obliqua* (Gabb); de Greve: 40; pl. 7, figs 5, 9, 12, 14, 23.
. 1945 *Pachydon obliqua* Gabb; Vokes: 21; pl. 4, figs 11–15.
. 1966 *Anisothyris obliqua* (Gabb); Willard: 65–69; pl. 57, figs 2, 3.
. 1969 *Pachydon obliqua* Gabb; Keen *in* Moore: N697, fig. E158, 7a–e.

TYPE MATERIAL. Not Studied. Late Caenozoic; Pebas, Peru (Gabb 1869). (ANSP, lost, not mentioned by Richards, 1968).

MATERIAL STUDIED. All late Caenozoic, Pebasian. L27749 (figured Woodward, 1871: pl. 5, figs 5a, b), Pichana, Peru, Hauxwell colln; L27750–2; L27703–11 (details as above, about 300 specimens). LL28008/1–7, Canamá, Brazil, juvenile valves, extracted from matrix, 1984 (C. Barrington Brown colln).

FURTHER RECORDS. Pebas (Gabb 1869, Boettger 1878, de Greve 1938, Willard 1966); Pichana (Conrad 1871*b*); Iquitos (de Greve 1938). Rio Marañon, 10 km upstream from Iquitos; 30 km north of Iquitos; Negro Urca, 200 km north of



Figs 358–361 *Pachydon obliquus* Gabb. Pebasian; Pichana, Peru; Hauxwell Colln. **358**, L27703; right valve internal, × 4. **359**, L27705; a, b, bivalved specimen viewed from left and front, × 3. **360**, L27704; left valve internal, × 4. **361**, L27706; a, b, juvenile specimen viewed from left side and front, × 15.

Iquitos; Rumi Tuni, on Rio Napo, 225 km north of Iquitos; 100 km south of Contamana on Rio Ucayali (all Willard 1966). Late Caenozoic, Pebasian, Upper Amazon Basin only.

DIAGNOSIS. Moderate-sized *Pachydon* with very incurved, prosogyrous umbones; generating curve oval; both valves *Glossus*-shaped, but with weak posterior ridges; highly inequivalve, with left valve much the smaller and right valve margin overlapping left; cardinal tooth of right valve very large, hooked, elongate, with correspondingly shaped socket in left valve; cardinal tooth not visible from outside when valves are closed; umbonal cavities present under hinge plates in both valves.

DESCRIPTION. The right valve is very tumid, the left valve has about half its convexity. The umbones, particularly that of the right valve, are prominent and very strongly incurved. Growth lines suggest that the right valve describes about one and a half whorls and the left only one whorl during growth to maximum convexity. Both figures are very high for bivalves in general. Lunule-like swellings occur under and anterior to the umbones in both valves, and the anterior surface of the cardinal tooth is not visible from the outside as it is in several other species assigned to the genus. Two posterior ridges are developed in each valve, those in the left being much the stronger. One ridge marks the posterior angulation, the other lies dorsal to it on the posterior area and is so weak that it can be seen only with difficulty. The highly polished shell surface is smooth, except for growth lines which give rise to some wrinkling. The commissures are curved and the right valve overlaps the left to a varying extent. The margin of the smaller left valve rests in a groove lying just inside the edge of the right valve. Both muscle scars and the pallial line are clearer in the less convex left valve. The pallial line is a broad, indistinct, band which lies comparatively far from the valve margins. The umbonal cavities under the hinge plates are very deep. The pedal muscle scars are difficult both to see and to interpret. In the right valve one, often deeply pitted, scar lies at the posterodorsal edge of the anterior adductor scar. This is probably the anterior pedal retractor scar. One, or sometimes two, deep scars lie just behind it on the buttress of the huge cardinal tooth. This may mark the pedal elevator. Scars are situated in similar positions in the left valve, within the anterior adductor scar and on the underside of the hinge plate underneath the anterior half of the cardinal socket. No distinct part of the posterior adductor scar can be recognized as the site of the posterior pedal retractor scar. The resilium pits are falciform or lanceolate. That in the right valve lies along the posterodorsal margin of the socket behind the cardinal tooth. The left resilifer is situated in a groove running parallel to the valve margin and lies dorsal to a somewhat angular ridge marking the posterodorsal edge of the cardinal socket.

	rv			lv			both valves br
DIMENSIONS. In mm.	l	h	br	l	h	br	
L27749, fig'd Woodward, 1871: pl. 5, fig. 5	16.5	15.2	–	–	–	–	11.3
L27750	18.5	14.8	–	–	–	–	11.2
L27751	18.9	15.5	8.5	15.2	11.4	5.2	10.7
L27752	18.3	14.2	8.5	15.6	11.5	5.1	10.7

All specimens listed above are from Pichana (Hauxwell Colln).

Note. The sum of the breadth of the left and right valves is greater than that of the shell breadth measured with the two valves fitted together: this is because of the curvature of the commissure

REMARKS. In this species the pallial line is comparatively far away from the valve margins. The umbonal cavities are, however, relatively large. This suggests that the mantle cavity is of normal volume with much of the available space for the soft parts lying in the umbonal cavities themselves.

Pachydon obliquus is one of the more inequivalve members of the genus. It is most similar to *P. carinatus* (Conrad), from which it may be distinguished by its highly incurved umbones. In addition, the latter is more elongate, more inequivalve and also has stronger and truly angular posterior ridges as well as a more strongly curved commissure.

Boettger (1878: pl. 14, figs 16, 17) figured a shell from Pebas that he considered to be transitional between *P. obliquus* and *P. carinatus*. From his illustration, it appears to lie within the normal range of *P. obliquus*, and there are no transitional forms between these two species in the large BMPD series from Pichana. *P. tenuis* Gabb and *P. cuneatus* Conrad resemble *P. obliquus* in having fairly smooth oval outlines, so incomplete specimens of these three species might be confused. However, the less incurved umbones of the two former species are an immediate distinction. In addition, *P. tenuis* is much more elongate-oval and far less inequivalve. *P. cuneatus* is equivalve and with a distinctly attenuated posterior. *P. obliquus* is the most common species of the genus in the Hauxwell Collection from Pichana.

The species was not previously recorded from Canamá: the specimens cited here were all obtained from washings of matrix mainly surrounding specimens of *Mytilopsis*. The specimen (L27749) figured by Woodward (1871) is deformed by growth halts in both valves accompanying a slight change of direction of growth. Other shells are figured herein: internal features are illustrated by valves from different specimens as it proved impossible to find a suitably well preserved conjugate individual.

Pachydon tenuis Gabb, 1869 Figs 362–367

*. 1869 *Pachydon tenua* Gabb: 199; pl. 16, figs 6, 6a.
. 1871*b* *Pachydon tenuis* Gabb; Conrad: 196; pl. 10, figs 1, 1a.
*v 1871*b* *Pachydon ovatus* Conrad: 197; pl. 10, fig. 4.
*v 1871 *Anisothyris hauxwelli* Woodward: 105; pl. 5, figs 7a–d.
v. 1871 *Anisothyris hauxwelli* var.α *distorta* Woodward: 105.
v. 1871 *Anisothyris hauxwelli* var.β *crassa* Woodward: 105.
. 1872 *Corbula (Anisothyris) tenuis* (Gabb) Dall: 91.
? 1874*b* *Pachydon tenuis* Gabb; Conrad: 83; pl. 12, fig. 5.
. 1878 *Anisothyris tenuis* (Gabb) Boettger: 499; pl. 14, figs 1–8 [see text, not *A. cuneatus* as indicated in plate explanation].
1879 *Anisothyris tenuis* (Gabb); Etheridge: 83.
1879 *Anisothyris hauxwelli* Woodward; Etheridge: 83.
. 1906 *Pachydon tenuis* Gabb; Clarke: 133.
v. 1906 *Pachydon ovatus* Conrad; Clarke: 133.
. 1924 *Anisothyris hauxwelli* Woodward; Roxo: 44.
. 1938 *Anisothyris tenuis* (Gabb); de Greve: 32; pl. 6, figs 1–3, 5, 9–15.
1966 *Anisothyris hauxwelli* Woodward; Willard: 66.
. 1966 *Anisothyris* cf. *hauxwelli* Woodward; Willard: pl. 57, fig. 4.
1966 *Anisothyris tenuis* (Gabb); Willard: 68.
. 1966 *Anisothyris* cf. *tenuis* (Gabb); Willard: pl. 58, fig. 1.
. 1968 *Pachydon tenuis* Gabb; Richards: 89.

HOLOTYPE of *P. tenuis* Gabb, ANSP 20061; Late Caenozoic, Pebasian; Pebas, Peru, Orton colln. (Richards, 1968: 89; not seen, since lost).

Holotype of *P. ovatus* Conrad, NYSM 8966; Late Caenozoic, Pebasian; Pichana, Peru, Hauxwell colln.

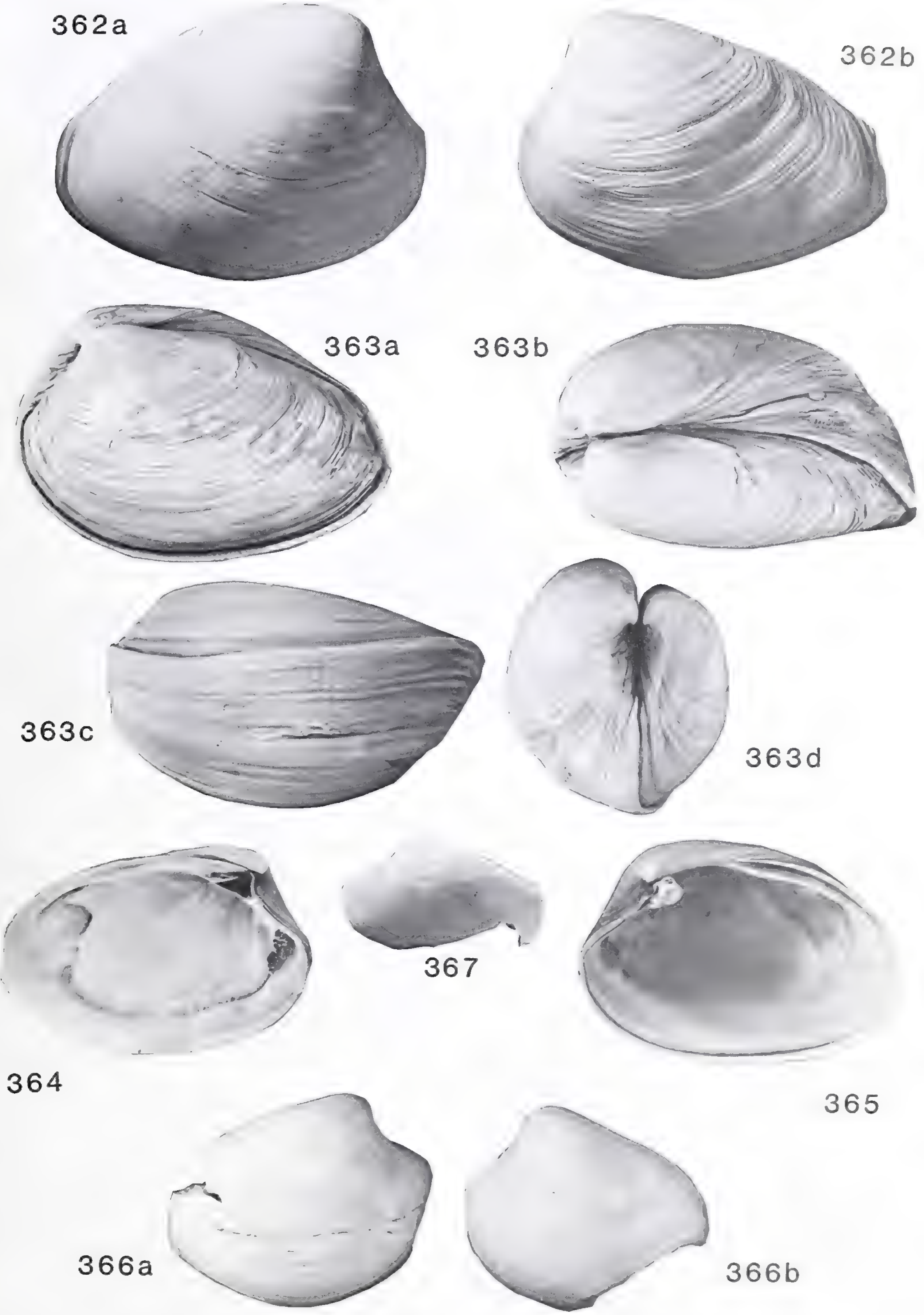
OTHER MATERIAL STUDIED. All Late Caenozoic, Pebasian; Pichana, Peru, Hauxwell colln. BMPD L27730, both valves of shell figured by Woodward (1871: pl. 5, figs 7a–d) as *Anisothyris hauxwelli* nom. nov. for *Pachydon tenua* Gabb; L27712–19; L27732–5 (about fifty specimens). LL27959/1–3, three broken juvenile valves, Puerto Nariño, Weeda colln.

FURTHER RECORDS. All Late Caenozoic, Pebasian; Pebas (Gabb 1869, Boettger 1878, Willard 1966: 68); Canamá (Etheridge 1879); Três Unidos (Roxo 1924); Iquitos (de Greve 1938, Willard 1966: pl. 58, fig. 1); on Rio Marañon, 10 km upstream from Iquitos (Willard 1966: pl. 57, fig. 4). Unlocalized (Conrad 1874*b*). Late Caenozoic, Pebasian only, Upper Amazon Basin.

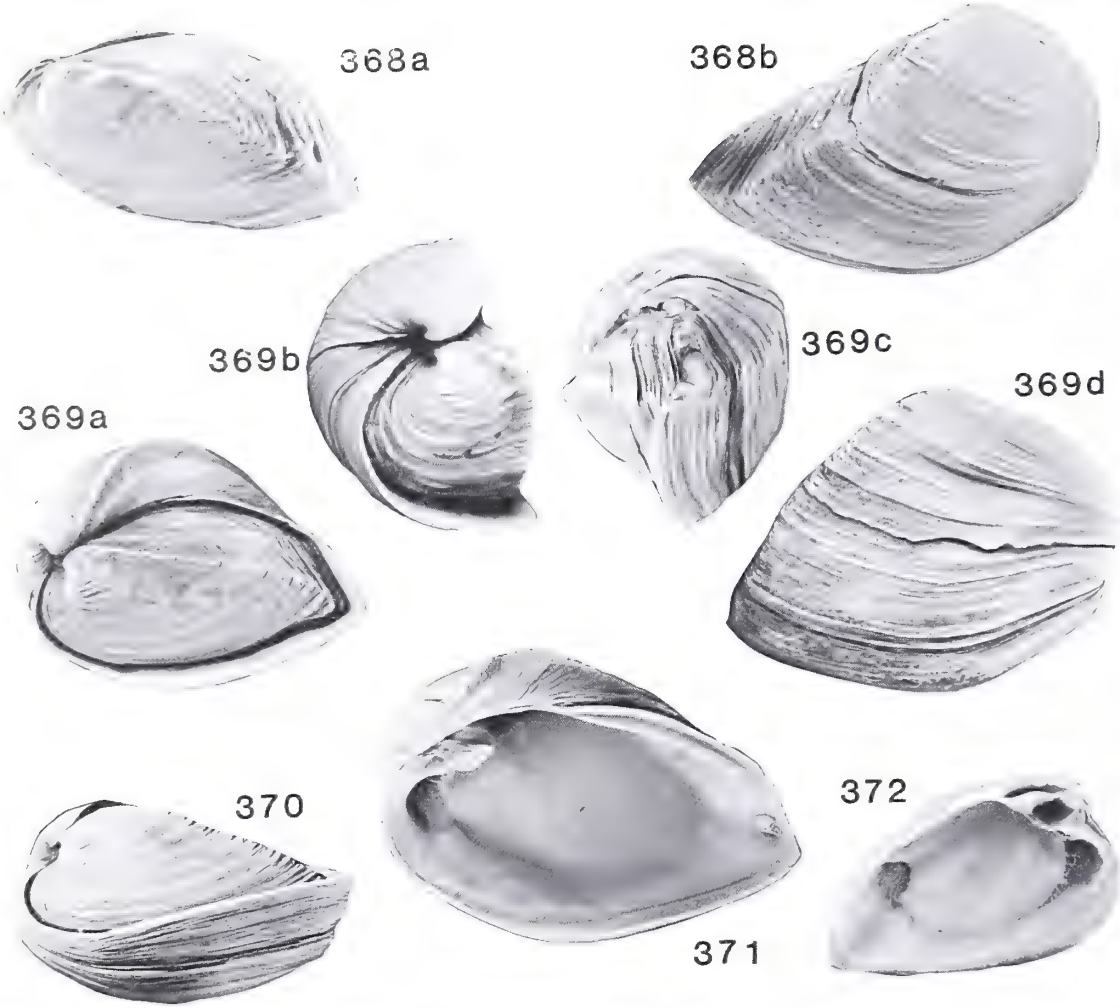
DIAGNOSIS. Large inequivalve *Pachydon* with smoothly elongate oval outline; commissure sinuous; left valve only just overlapped by rim of right valve; anterior surface of cardinal tooth visible from outside when viewed from front.

DESCRIPTION. The shell surface is shiny and smooth except for growth lines. There are few traces of radiating sculpture. There is a faint ridge running from the umbo to the most anterior point of the left valve. In the right valve there is a groove marking the edge of the lunule and also two ridges running posteriorly from the umbo; the latter are in the same position as those in *P. carinatus* (p. 296) but very faint, not forming an angulation isolating a posterior area or corselet. The internal features are broadly similar to those of *P. obliquus* (p. 292), with the left hinge plate attached to the dorsal margin of the valve, but with the pallial line lying nearer the ventral margin in both valves. A pair of anterior retractor scars are situated behind and above the anterior adductor scar in the right valve. In the left valve the retractor scars are at the ventral surface of the anterior end of the hinge plate. The pedal elevator scars are best seen in rather small, less tumid shells in which much of the umbonal cavity is visible; they leave a line of small scars underneath the central and rear part of the hinge plate in the left valve. In the right valve a single, larger and deeper, scar is present underneath that part of the hinge plate underlying the ligamental socket behind the cardinal tooth. The posterior pedal retractor scar coalesces with the anterodorsal margin of the posterior adductor.

DIMENSIONS. In mm. (All Pichana).	rv			lv			br both valves
	l	h	br	l	h	br	
L27730, figured Woodward, 1871: pl. 5, fig. 7.	40.8	30.0	15.5	39.6	29.0	12.4	27.8
L27712	30.0	21.2	–	–	–	–	18.4
L27713	26.0	18.0	10.0	–	–	–	–
L27714	–	–	–	25.0	17.5	7.1	15.0
Holotype of *P. ovatus*, NYSM 8966	27.6	22.9	–	25.9	22.1	–	–



Figs 362–367 *Pachydon tenuis* Gabb. Pebasian. **362–366**, Pichana, Peru; Hauxwell Colln. **362**, L27730; shell figured by Woodward (1871: pl. 5, fig. 7) as *Anisothyris hauxwelli* nom. nov.; a, b, left, right valve, × 1.5. **363**, L27712; a–d, left, dorsal, ventral, front views, × 2. **364**, L27714; left valve internal, × 2. **365**, L27713; right valve internal, × 2. **366**, NYSM 8966; holotype of *Pachydon ovatus* Conrad. a, b, left, right valves, × 1.5. **367**, LL27954/1; Puerto Nariño, Colombia; Weeda Colln. Broken left valve with umbonal region tilted towards camera to show early stages of shell; × 4.



Figs 368–372 *Pachydon carinatus* Conrad. Pebasian; Pichana, Peru; Hauxwell Colln; all × 2. **368**, L27720; specimen figured by Woodward (1871: pl. 5, fig. 6); a, b, left, right valves. **369**, L27722; a–d, viewed from left, front, rear, and right. **370**, L27721; ventral view. **371**, LL28136; right valve internal. **372**, L27723; left valve internal.

REMARKS. *P. tenuis* is rather similar in general shape to *P. carinatus* Conrad but lacks the posterior angulation and has virtually obsolete radiating ribs. *P. cuneatus* Conrad is equivalve and its umbones are much nearer the anterior. A comparison with *P. obliquus* Conrad is given under the latter, p. 294. *P. tenuis* is the largest species of *Pachydon* with the exception of *P. erectus* Conrad, and is plentifully represented in the BMPD collections from Pichana. Woodward (1871) proposed the name *Anisothyris hauxwelli* as a replacement for *P. tenuis* Gabb, on the unjustified grounds that Gabb's specific name was inappropriate and therefore misleading. Woodward's 'varieties' *distorta* and *crassa* do not appear to merit separation from *P. tenuis*, s.str., and are not figured herein. *P. ovatus* Conrad is clearly the same as *P. tenuis*. Although Etheridge (1879) recorded this species as occurring at Canamá, no specimens from there were ever acquired by BMPD: some doubt must exist about his record. The specimen figured by Willard (1966: pl. 58, fig. 1) does not show the specific characters clearly, though his other illustration as *A.* cf. *hauxwelli* (pl. 57, fig. 4) undoubtedly belongs to *tenuis*.

Pachydon carinatus Conrad, 1871 Figs 368–373

* 1871*b* *Pachydon carinatus* Conrad: 196; pl. 10, fig. 7.
v. 1871 *Anisothyris carinata* (Conrad) Woodward: 106; pl. 5, fig. 6.
. 1872 *Anisothyris carinata* (Conrad); Dall: 89.
. 1878 *Anisothyris carinata* (Conrad); Boettger: 501; pl. 14, figs 23–27.
1879 *Anisothyris carinata* (Conrad); Etheridge: 83.
. 1906 *Pachydon carinatus* Conrad; Clarke: 132.
1924 *Anisothyris carinata* (Conrad); Roxo: 44.
. 1938 *Anisothyris carinata* (Conrad); de Greve: 43; pl. 9, figs 1–3, 6, 7.
? 1966 *Anisothyris carinata* (Conrad); Willard: 65, 67, 68.
. 1966 *Anisothyris cuneata* (Conrad); Willard: pl. 57, fig. 1.

TYPE MATERIAL. Late Caenozoic, Pebasian; Pichana, Peru, Hauxwell colln (NYSM; Clarke 1906). Not studied.

MATERIAL STUDIED. L27720, figured Woodward (1871: pl. 5, fig. 6); L27721–3, L27727–9 (about 20 specimens), LL28136–40; all late Caenozoic; Pichana, Peru, Hauxwell colln.

FURTHER RECORDS. All late Caenozoic. Pebas (Boettger 1878); Canamá (Etheridge 1879); Três Unidos (Roxo 1924); Iquitos (de Greve 1938). Rumi Tuni (Willard 1966: pl. 57, fig. 1, as *A. carinata*). Other unfigured records from the Iquitos area (Willard 1966) are doubtful. Late Caenozoic, Upper Amazon Basin only.

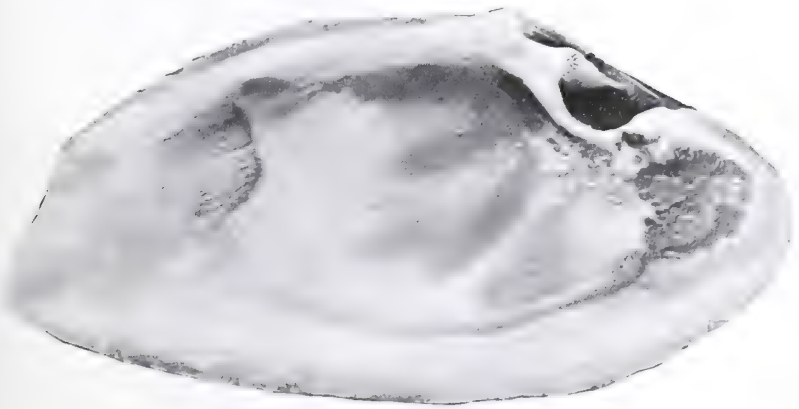


Fig 373 *Pachydon carinatus* Conrad. Pebasian; Pichana, Peru; Hauxwell Colln. LL28137; left valve interior showing row of pits, interpreted as pedal elevator scars, lying along junction between hinge plate and floor of valve; × 4.

DIAGNOSIS. Moderately large *Pachydon* with strong carina separating flank from posterior area in both valves; secondary carina on posterior areas also present; inequivalve, with ventral margin of smaller left valve resting inside strongly curved rim of right valve; umbones prosogyrous, incurved and pointed; anterior surface of cardinal tooth barely visible from outside; outline elongate oval but with angular junction between ventral and posterior margins; deep umbonal cavity formed in tumid right valve; no umbonal cavity in left valve.

DESCRIPTION. The commissure of the right valve is strongly twisted along all margins, but that of the left valve, which sits within the right valve, is less so. The posterior area or corselet of the right valve is so curved that it is barely visible in side view. The pallial line runs in a curve between the inner and ventral margins of the two adductor scars. The posterior pedal retractor scar is just visible above the posterior adductor scar. The anterior pedal retractor scar in the right valve occurs low on the buttress below the cardinal tooth, fairly close to the anterior adductor scar. In the left valve, two or three irregular and pock-marked scars are situated on the ventral surface of the hinge plate in front of the cardinal socket. No umbonal cavity is present in the left valve; instead, the hinge plate is attached to the floor of the valve rather than being suspended from its dorsal margin as in the right valve. Thus, in the left valve a series of up to a dozen small, sometimes coalescing, scars may be seen along this junction of hinge plate and valve floor. These are interpreted as pedal elevator scars. No such scars can be seen in the more tumid and incurved right valve.

DIMENSIONS. In mm. (All Pichana).	rv			lv			br both valves
	l	h	vbr	l	h	vbr	
L27720, fig'd Woodward, 1871.	27.6	19.0	12.4	23.8	13.1	6.4	13.2
L27721	23.0	14.2	–	–	–	–	12.5
L27722	25.5	18.2	–	–	–	–	14.0
L27723	–	–	–	20.0	12.3	5.8	–

REMARKS. Differences between this species and *P. obliquus* are given under the latter, p. 294. Differences in their muscle scar pattern are probably because the left valve of *P. carinatus* is comparatively flat.

Pachydon erectus Conrad, 1871 Figs 374–384

*v	1871*b*	*Pachydon erectum* Conrad: 197; pl. 10, fig. 16 (two figures).
*v	1871*b*	*Pachydon altus* Conrad : 197; pl. 11, fig. 1.
v.	1871	*Anisothyris erecta* (Conrad) Woodward : 107; pl. 5, figs 9a, b.
.	1874*a*	*Pachydon altus* Conrad; Conrad : 28; pl. 1, figs 4, 18.
.	1878	*Anisothyris erecta* (Conrad); Boettger : 500; pl. 14, figs 12, 13.
*v	1879	*Corbula canamaensis* Etheridge : 84; pl. 7, figs 3, 3a.
v.	1906	*Pachydon altus* Conrad; Clarke : 132.
v.	1906	*Pachydon erectus* Conrad; Clarke : 133.
.	1938	*Anisothyris erecta* (Conrad); de Greve : 36, pl. 8, figs 1–3, 8.
.	1938	*Anisothyris erecta* (Conrad)–*Anisothyris tenuis* (Gabb); de Greve: pl. 7, figs 1, 6.
.	1966	*Anisothyris erecta* (Conrad); Willard : 65–69 (*pars*); pl. 58, fig. 2.
v.	1982	*Anisothyris erectus* (Conrad); Nuttall *in* Bristow & Parodiz: 20.

HOLOTYPE of *P. erectus* Conrad, 1871, NYSM 8964, the right valve figured by Conrad 1871: pl. 10, fig. 16, right figure, an external view. Late Caenozoic; Pichana, Peru (Hauxwell colln). The left figure is an internal view of a left valve, apparently of the same specimen; it has not been seen and its whereabouts are unknown. Conrad stated that he had only one specimen of this species and that the valves were much less unequal than in *P. obliquus* Gabb.

Holotype of *Pachydon altus* Conrad, 1871, NYSM 8961. Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln).

Lectotype, selected herein, of *Corbula canamaensis* Etheridge, 1879: BMPD LL27853, the specimen figured by Etheridge (1879). The accompanying unfigured shells, LL27854–6, 3 left and 1 right valves are paralectotypes. All Late Caenozoic, Pebasian; Canamá (C. Barrington Brown colln).

OTHER MATERIAL STUDIED. BMPD L27740, specimen figured by Woodward (1871: pl. 5, figs 9a, b) and the accompanying unfigured specimens, L27736–9, LL27844, LL28072; all Late Caenozoic, Pichana (Hauxwell colln); LL28080–5, Pichana, as above, but extracted from matrix 1982. LL27888, Loc. 33/480–560 cm; LL27890–6, Loc. 33/570–670 cm; LL27873, LL40802,

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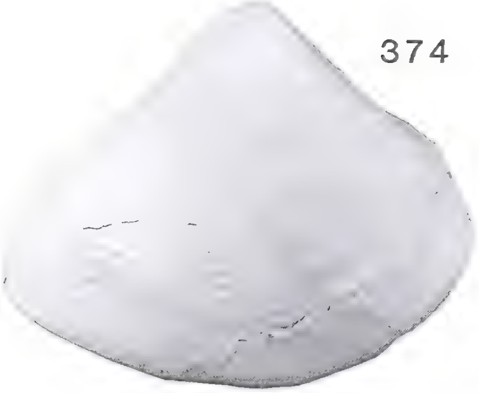

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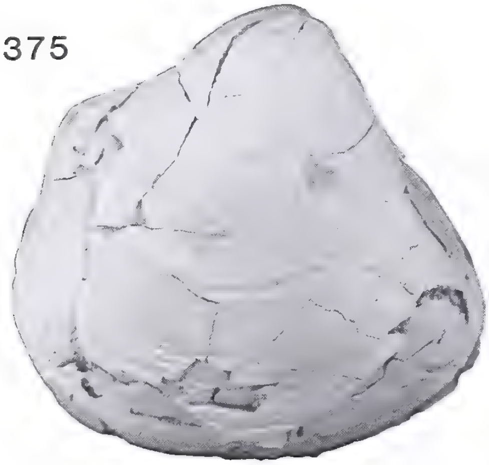

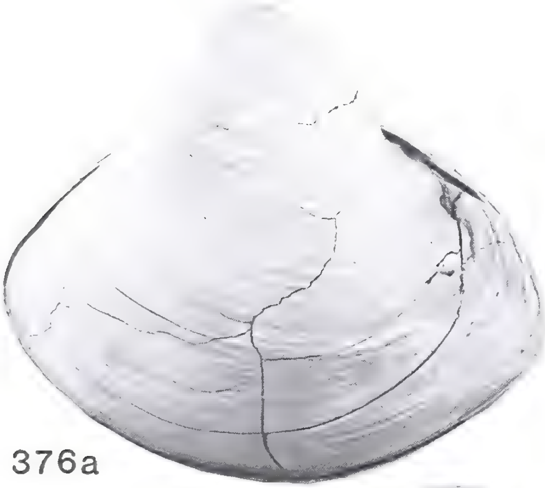

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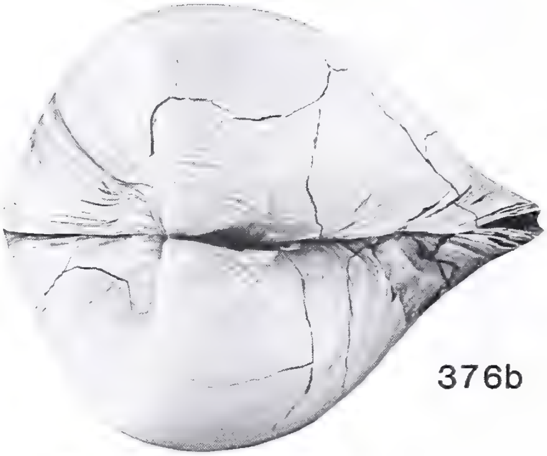

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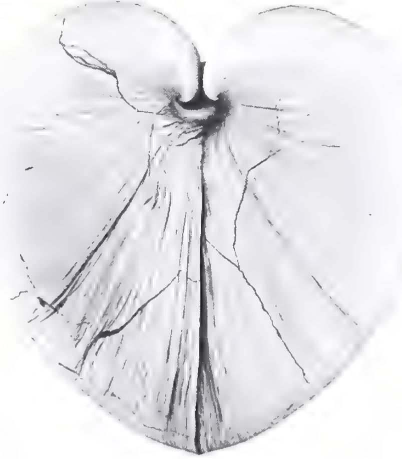

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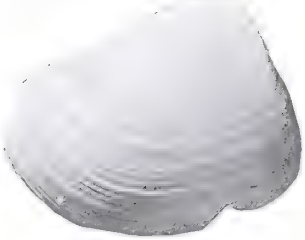

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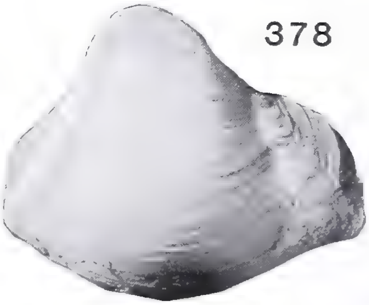


Figs 374–378 *Pachydon erectus* Conrad. Pebasian; Peru. **374–377**, Pichana; Hauxwell Colln. **374**, NYSM 8964; holotype of *Pachydon erectus* Conrad, figured by Conrad (1871: pl. 10, fig. 16); single right valve, × 1.5. **375**, NYSM 8961; holotype of *Pachydon altus* Conrad, figured by Conrad (1871: pl. 11, fig. 1); right valve, × 1.5. **376**, L27740; shell figured by Woodward (1871: pl. 5, fig. 9) as *Anisothyris erecta*; a–c, left, dorsal and front views, × 1.5. **377**, LL27844; juvenile shell, right valve, × 2.5. **378**, LL27853; **lectotype** (herein selected) of *Corbula canamaensis* Etheridge, figured by Etheridge (1879: pl. 7, fig. 3); Canamá, Barrington Brown Colln. Left valve, × 2.5.

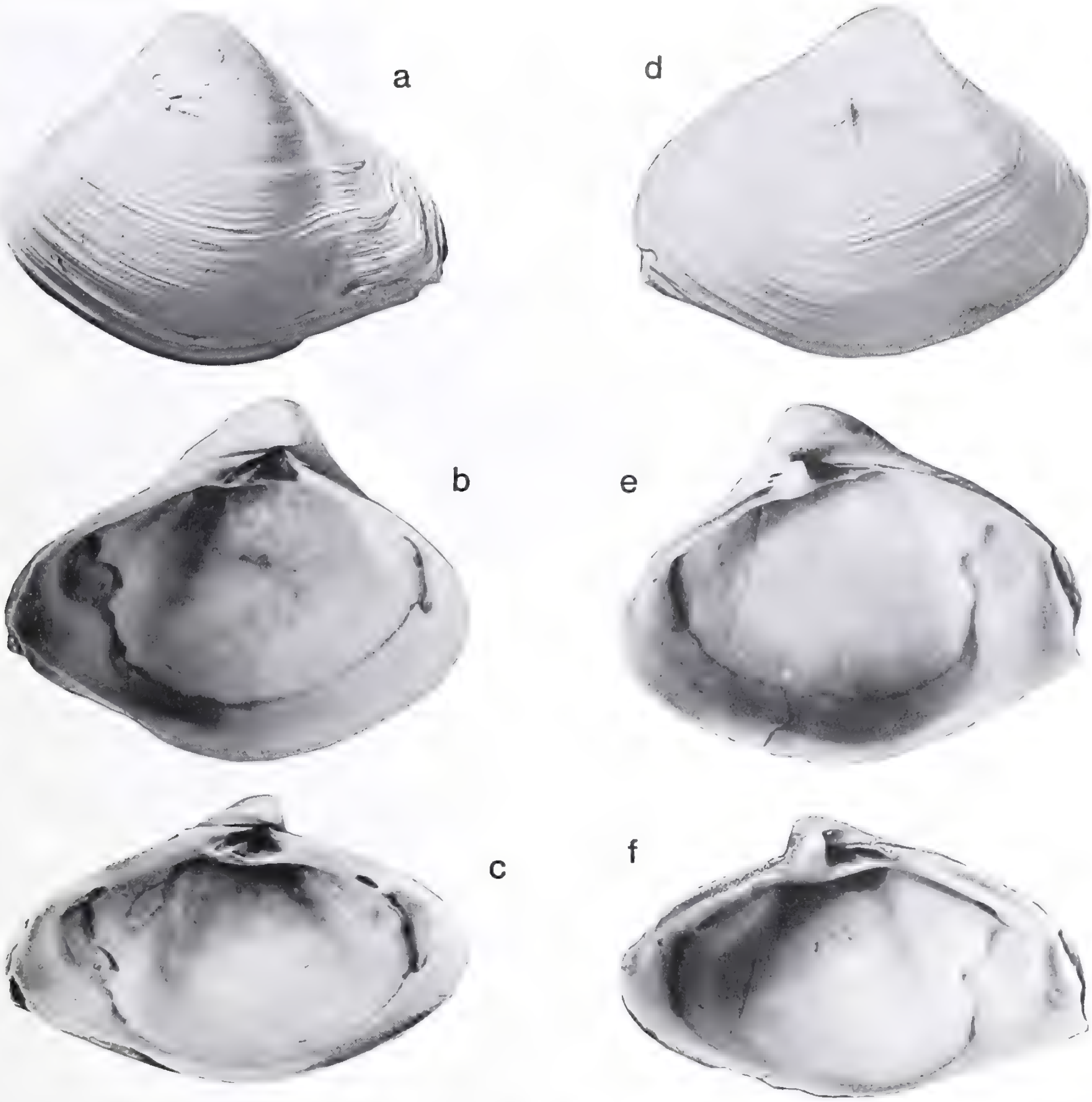


Fig. 379 *Pachydon erectus* Conrad. L27738; Pebasian; Pichana, Peru; Hauxwell Colln. a–f, left and right valves, external, internal normal and oblique views, × 2.5.

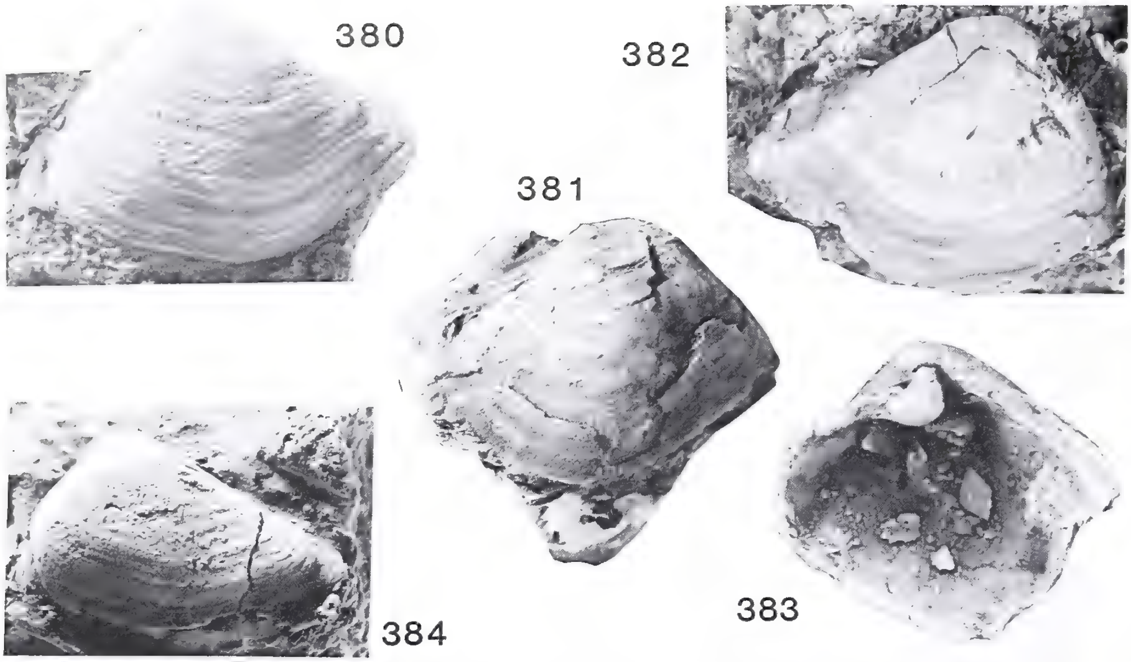
Loc. 45; LL27874–8, Loc. 54; all Late Caenozoic, La Tagua (Eden colln).

FURTHER RECORDS. Pebas (Conrad 1874*a*, Boettger 1878, de Greve 1938); Iquitos (de Greve 1938); Pebas, Iquitos, Rumi Tuni and Rio Aguaytia 25 km from confluence with Rio Ucayali (Willard 1966).

DISTRIBUTION. Late Caenozoic, Pebasian; Upper Amazon Valley. Late Caenozoic; La Tagua, Colombia.

DIAGNOSIS. Large, tumid, equivalve *Pachydon*; subtrigonal with short anterior, posterior alate, slightly upturned; corselet crassatelliform; umbones very prominent and strongly curved; front of cardinal tooth external.

DESCRIPTION. In smaller, slim, specimens, such as those from La Tagua, the anterior appears comparatively elongate with the anterodorsal margin sloping forward and downward in a mildly convex curve. In very tumid adults, such as those figured by Conrad (1871*b*) and Woodward (1871), this margin forms a concave curve and the shell will balance on this broad flattened area. The change of appearance can be explained as a result of normal spiral growth of a shell with large, strongly incurved, prosogyrous umbones, producing an abnormally high angular displacement of the earlier-formed parts of the shell compared with the majority of bivalves. Internal views show that the generating curves in this species are similar in shape regardless of shell size. The ventral margin may be either evenly convex or drawn out into an elongate posterior extension which is differentiated weakly from the main flank of the shell by a broad, shallow, sulcus. The posterodorsal margin tends to be crassatelliform to a varying extent. The zone nearest to this margin is vaguely distinct from the rest of the shell but is rarely separated as a corselet by a radiating ridge. The most anterior and posterior extremities of the shell lie well below mid-height and the umbones lie forward of mid-length. The lowest point of the ventral margin is slightly posterior to mid-length of the shell and corresponds with a slight fold in the commissure of the right valve and sulcus in the left. The adductor scars are subcircular with identations on their inner margins marking the separation into 'quick' and 'catch' attachment scars (Cox, *in* Moore 1969: N35). Anterior and posterior pedal retractor scars are situated



Figs 380–384 *Pachydon erectus* Conrad. Late Caenozoic; La Tagua, Colombia; Eden Colln. **380**, LL27890; Loc. 33/570–670, left valve, × 5. **381**, LL27893; Loc. 33/570–670, right valve, × 3. **382**, LL27877; Loc. 54, right valve, × 3. **383**, LL27874; Loc. 54, right valve internal view, × 5. **384**, LL40802; Loc. 45, latex cast of internal mould of left valve, × 4.

immediately dorsal to the adductors and in some specimens the anterior scar can be seen to have two parts, the one nearer the umbo being the larger. The pallial sinus is notched posteriorly, meeting the posterior adductor at its forward lower margin.

DIMENSIONS. In mm.	l	h	br	l/h	br/l
Lectotype of *P. erectus* Conrad. NYSM 8964, Pichana	40.0	32.8	15.3 (sv)	1.22	0.77
Lectotype of *P. altus* Conrad. NYSM 8961, Pichana	–	38.5	32.0	–	–
Shell figd. Woodward, 1871: pl. 5, fig. 9. L27740, Pichana	49.0	44.2	39.3	1.11	0.80
Lectotype of *Corbula canamensis* Etheridge. LL27853, Canamá	19.5	15.5	7.8 (sv)	1.25	0.80
L27736, Pichana	35.7	26.8	12.6 (sv)	1.33	0.71
L27737, Pichana	23.2	18.3	7.5 (sv)	1.27	0.65
LL27844, Pichana	15.7	13.3	6.0 (sv)	1.18	0.76
LL27877, Loc. 54, La Tagua	16.3	12.3	–	1.33	–
LL27890, Loc. 33/570–670, La Tagua	9.8	6.9	–	1.42	–

Note. (sv) = single valves only.

REMARKS. The reasons for regarding NYSM 8964 as the holotype of *P. erectus* are given above. Conrad also appears to have had only one specimen of *P. altus*. In his description of it, he said the shell was silicified, and that the internal mould was of indurated ferruginous clay. The posterior of NYSM 8961 is missing, thus revealing the infilling matrix and the apparently normal but worn aragonitic shell, which probably explains Conrad's reference to the internal mould and his belief that the shell was silicified.

P. erectus is the largest species of the genus known. Features distinguishing it from other almost equivalve species such as *P. cuneatus* Conrad, *P. hettneri* (Anderson) and *P. trigonalis* sp. nov. (p. 309) are its both erect and strongly incurved umbones, its alate posterior and its crassatelliform corselet. *P. iquitensis* (de Greve 1938: 46; pl. 5, figs 38–41), known only from a single right valve from Iquitos, is fairly similar but has a lower and less incurved umbo and also lacks the crassatelliform corselet typical of *P. erectus*.

Study of type material of *P. altus* Conrad and *P. canamaensis* (Etheridge) shows that both are synonyms of *P. erectus*. De Greve (1938: pl. 7, figs 1, 6) illustrates a left valve from Iquitos which he named as '*Anisothyris erectum* Conrad – *Anisothyris tenuis* Dall'. It is a typical *P. erectus* and shows no features characteristic of *P. tenuis*.

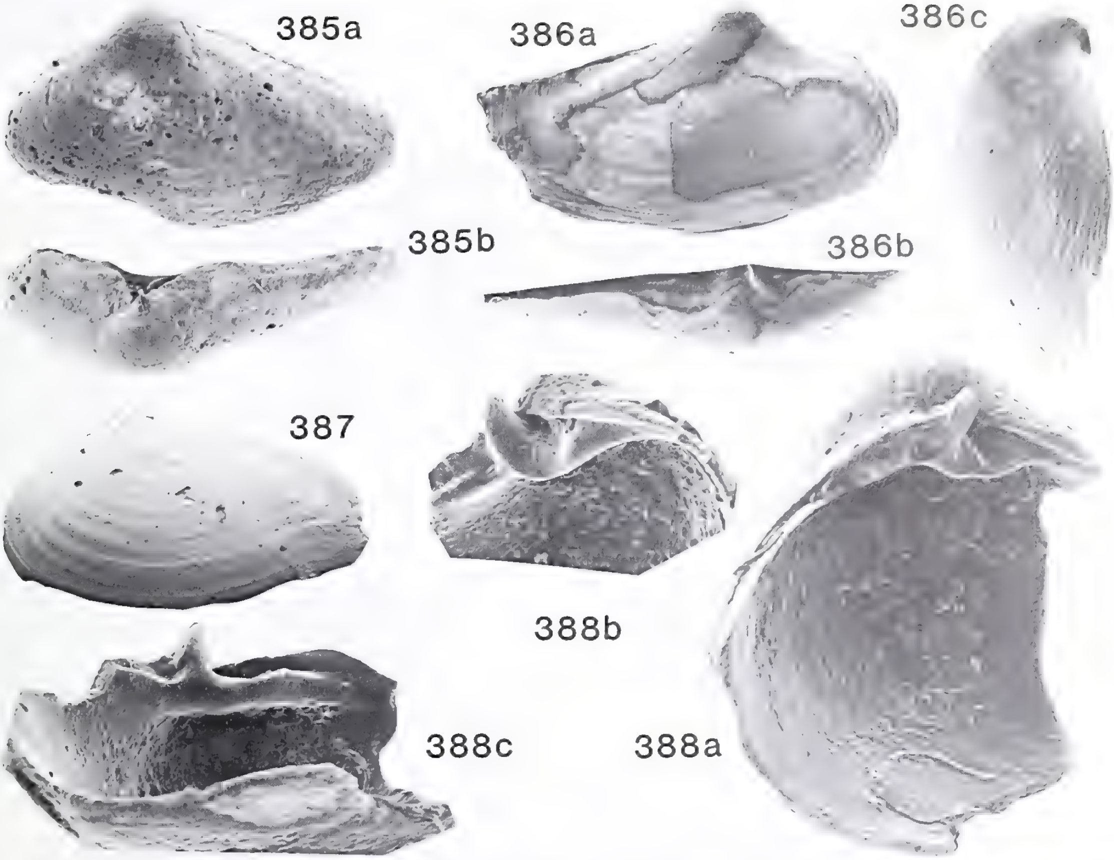
Some doubt exists about Willard's (1966) records. He figured two shells, both from Pebas. His pl. 58, fig. 2 is correctly identified, but his pl. 58, fig. 3, the interior of a right valve, is of a different, unidentifiable species.

Pachydon erectus elongatus (Boettger, 1878)

Figs 385–388

* 1878 *Anisothyris erecta* (Conrad) var. *elongata* Boettger: 500; pl. 14, figs 14, 15.
. 1938 *Anisothyris erecta* (Conrad) var. *elongata* Boettger; de Greve: 38; pl. 7, fig. 13; pl. 8, figs 4, 5.

LECTOTYPE (selected de Greve 1938: 40). The specimen figured by Boettger (1878: pl. 14, fig. 14) and again by de Greve (1938: pl. 7, fig. 13; pl. 8, fig. 5). The original of Boettger's (1878) pl. 14, fig. 15, refigured by de Greve (1938: pl. 8, fig. 4), is a paralectotype. Both Late Caenozoic, Pebasian;



Figs 385–388 *Pachydon erectus elongatus* (Boettger). Pebasian; Pichana, Peru; Hauxwell Colln. **385**, LL28083; a, b, left valve, side and dorsal views, × 10. **386**, LL28081; a, right valve, side, × 10; b, dorsal view, × 10; c, front, × 20. **387**, LL28080; left valve, × 10. **388**, LL28082; a–c, internal views of broken right valve, all × 30.

either Pebas or Pichana, Peru (Hauxwell colln). In Senckenburg Museum, Frankfurt (not studied).

Material studied. BMPD LL28080–5, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln, extracted from matrix, 1982). No further records.

Distribution. Restricted to Pebasian. Pebas or Pichana (Boettger 1878); Iquitos (de Greve 1938); probably Pichana (herein).

Diagnosis. Differing from *Pachydon erectus* Conrad, s.str., in being very small and elongate, with a length to height ratio of more than 1.5:1.

Dimensions. In mm.	l	h	br	l/h
Lectotype, Boettger's (1878) pl. 14, fig. 14, ? Pebas or Pichana.	5.6	3.6	–	1.59
Paralectotype, Boettger's (1878) pl. 14, fig. 1, ? Pebas or Pichana.	7.0	4.4	–	1.56
Iquitos (de Greve 1938: 40).	20.3	11.8	3.0 (sv)	1.72
Iquitos (de Greve 1938: 40).	18.9	11.1	4.4 (sv)	1.70
Iquitos (de Greve 1938: 40).	16.9	9.6	2.9 (sv)	1.76
LL28080, Pichana.	2.5	1.5	–	1.67
LL28081, Pichana.	6.2	2.5	1.15 (sv)	2.48

Note. The above measurements of Boettger's figured specimens are calculated from de Greve's illustrations. In his text (1938: 40), de Greve quotes a length of 7.5 mm and height of 4.5 mm for the lectotype. (sv) = single valve.

Description. The shell is small, apparently not exceeding 8 mm in length. The umbones are situated well anterior to mid-length of the shell. Outline crassatelliform, with a corselet separated from the main flank of the shell by a comparatively weak diagonal ridge of variable strength. The posterior tends to be truncated to some extent. The shell is virtually equivalve, and the commissure straight, as far as can be ascertained. In vertical view, the shell is rather stout.

Remarks. Unfortunately, there is no good, continuous, growth series of *P. erectus* available for study. However, the impression gained from the Hauxwell Collection is that there are a few small shells which are distinctly too elongate to be assigned to typical *P. erectus*. At the same time, they can be separated from the even more elongate *P. ledaeformis* (Dall) which is also noticeably slimmer in vertical view. *P. amazonensis* (Gabb) possesses much less prominent umbones. Boettger's decision, therefore, to regard his small specimens as representing a variety of *P. erectus* seems reasonable on the available evidence. Unfortunately, de Greve (1938) figured none of the distinctly larger Iquitos specimens, whose dimensions are repeated above.

Pachydon cuneatus Conrad, 1871 Figs 389–393

*v 1871*b* *Pachydon cuneatus* Conrad: 197; pl. 10, fig. 12.
v. 1871 *Anisothyris cuneata* (Conrad) Woodward: 107; pl. 5, figs 8a, b.

. 1874*a* *Pachydon cuneata* Conrad; Conrad: 28; pl. 1, fig. 3.
. 1878 *Anisothyris cuneata* (Conrad); Boettger: 500 (*pars*); pl. 14, fig. 11.
*v 1879 *Anisothyris* (*Pachydon*) *tumida* Etheridge: 83; pl. 7, fig. 2.
v. 1906 *Pachydon cuneatus* Conrad; Clarke: 133.
1924 *Anisothyris cuneatus* (Conrad); Roxo: 44.
. 1938 *Anisothyris cuneata* (Conrad); de Greve: 34; pl. 6, figs 4, 6–8, 16, 17; pl. 8, figs 18, 19.
1952 *Pachydon cuneatus* Conrad; Rutsch: 449.
? 1966 *Anisothyris cuneata* (Conrad); Willard: 66–68 (*pars*); pl. 59, figs 2, 3 (*non* fig. 1)

LECTOTYPE, selected herein, of *Pachydon cuneatus* Conrad, 1871: NYSM 8963, the right valve figured by Conrad (1871*b*). The unfigured left valve of another individual found with the lectotype is a paralectotype. Both Late Caenozoic, Pebasian; Pichana (Hauxwell colln).

Lectotype, selected herein, of *Anisothyris (Pachydon) tumida* Etheridge, 1879: BMPD LL27851, a left valve, probably that figured by Etheridge (1879). One complete bivalved shell and two separate right valves, LL27852/1–3, not figured, are paralectotypes. All Late Caenozoic, Pebasian; Canamá (C. Barrington Brown colln).

OTHER MATERIAL STUDIED. BMPD L27725, specimen figured by Woodward (1871: pl. 5, figs 8a, b) and accompanying unfigured specimens, L27724, L27726/1–2, LL27845; all Late Caenozoic, Pebasian; Pichana (Hauxwell colln); LL28078–9, two good left valves, and LL27857/1–4, three left and one right valves (all damaged); Late Caenozoic, Pebasian; Puerto Nariño, Colombia (Weeda colln).

FURTHER RECORDS. Late Caenozoic, Pebasian: Pebas, Peru (Boettger 1878, Willard 1966); either Pebas, Old Pebas or Pichana (Conrad 1874*a*); Iquitos, Peru (de Greve 1938); Negro Urca and ? Rumi Tuni, Peru (Willard 1966); Três Unidos, Peru and Tracaos on Rio Quixitos, Brazil (Roxo 1924). ? Yucales Formation, Santa Ines Group: State of Monogas, Guarico and Aragua, Venezuela (Rutsch 1952).

DISTRIBUTION. Late Caenozoic, Pebasian Basin of Upper Amazon Valley and ? Late Caenozoic of Venezuela.

DIAGNOSIS. Virtually equivalve *Pachydon* with almost plane commissure; high, prosogyrous umbones placed well forward, above anterior adductor; outline subtrigonal, with posterodorsal and ventral margins forming comparatively smooth curves; cardinal tooth very prominent.

DESCRIPTION. Both the greatest height and greatest breadth are very close to the anterior, and in dorsal view the anterior of the shell appears very foreshortened. The large cardinal tooth is strongly hooked, directed forwards at about 45°, and its anterior surface has a prominent callosity which is exposed to the outside world. A comparatively strong right posterior lateral tooth is present. The right anterior lateral is no more than a weak ridge lying parallel to the anterior extension of the hinge plate. The pallial line is slightly truncated below the posterior adductor scar, but no definite sinus is formed.

DIMENSIONS. In mm.	l	h	br (sv)	l/h	br/l
Lectotype, NYSM 8963, Pichana	26.0	22.5	11.2	1.16	0.86
L27725, shell fig'd Woodward (1871: pl. 5, fig. 8), Pichana	30.0	24.8	24.0	1.21	0.80
L27724, Pichana	28.4	23.8	11.9	1.19	0.84
L27726/1, Pichana	24.8	21.4	10.0	1.15	0.81
L27726/2, Pichana	29.2	24.8	12.0	1.18	0.82
Lectotype of *Anisothyris tumida* Etheridge, LL27851, Canamá	17.9	14.5	6.2	1.23	0.69
LL28078, Puerto Nariño	14.9+	13.7	6.0	1.09+	0.81
LL28079, Puerto Nariño	10.8	9.4	3.5	1.15	0.62

Note. Breadth measurements are of single valves (sv). This is doubled for br/l calculations.

REMARKS. This is a very uncommon species, represented in BMPD collections by eight specimens from Pichana, five from Canamá and six from Puerto Nariño. The forward position of the umbones immediately distinguishes it from other almost equivalve species of *Pachydon*. The outline of *P. tenuis* Gabb, 1869, most closely resembles that of *P. cuneatus*, but its umbones are further back and it is inequivalve. In the very inequivalve *P. obliquus* Gabb, 1869, the umbones are even further forward.

A. (*P.*) *tumida* Etheridge, 1879, is clearly identical to *P. cuneatus* Conrad: Etheridge, however, gave no comparison between the two. Boettger's (1878) explanation of his plate 14 lists figs 1–11 as *A. cuneata*. This appears to be a misprint as his text (1878: 499, 500) shows that he rightly identified figs 1–8 as *A. tenuis* (Gabb). I consider that his figs 9 and 10 are probably juvenile *P. tenuis*, leaving only pl. 14, fig. 11 as *P. cuneatus*.

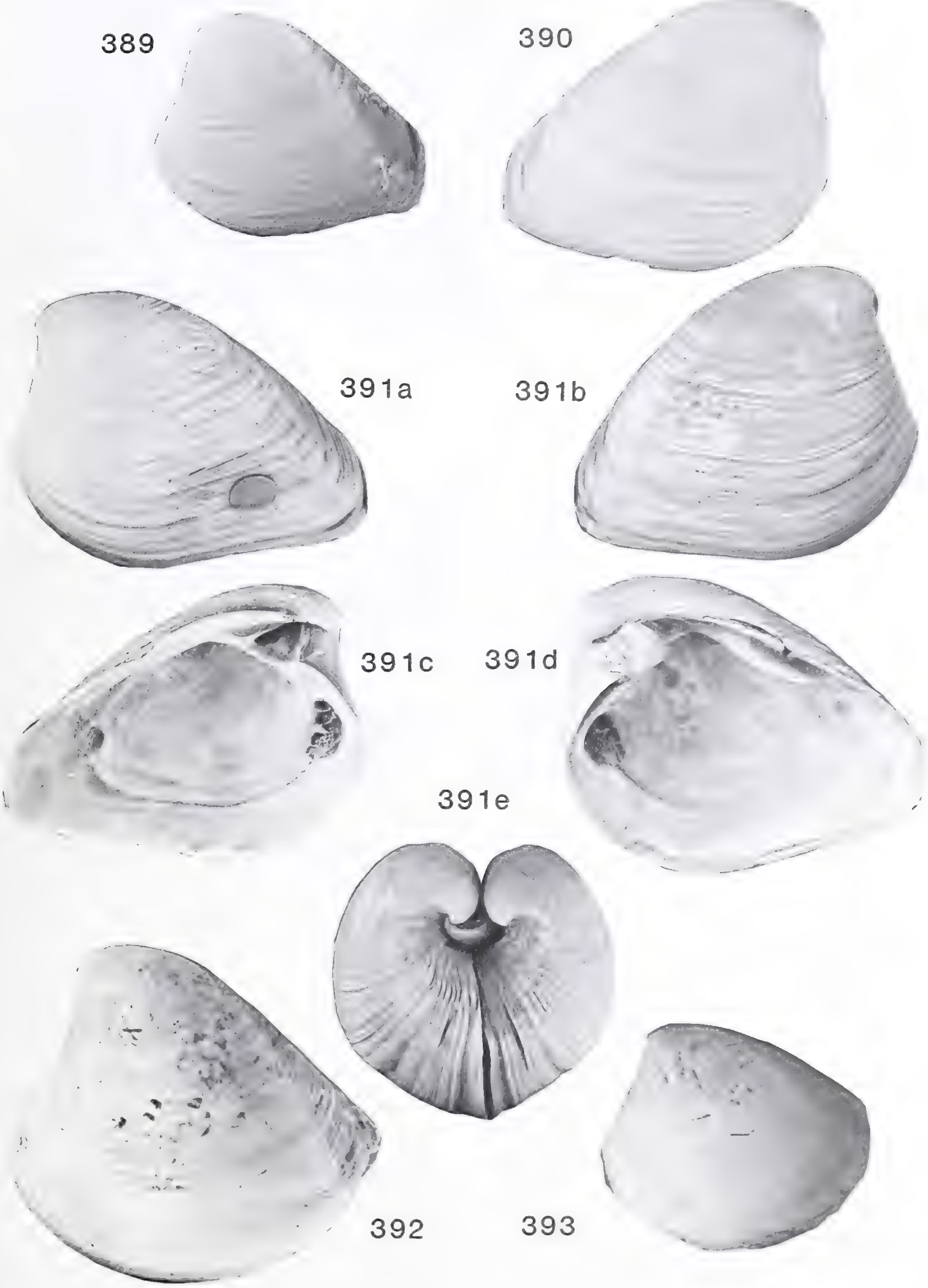
Willard's (1966) records need interpreting with some care. For example, the specimen from Rumi Tuni figured (his pl. 57, fig. 1) as *A. cuneata* is clearly *P. carinatus* Conrad: he lists both these species from this locality. On the other hand, his pl. 59, fig. 2 and probably fig. 3, from Pebas and Iquitos respectively, are correctly identified as *Anisothyris cuneata*. However, the latter figure is a posterodorsal and not an anterior aspect as stated and, in addition, in his text (1966: 65) he did not list the species as occurring at Iquitos.

Rutsch (1952) expressed some doubts about his identification of *P. cuneatus* from Venezuela.

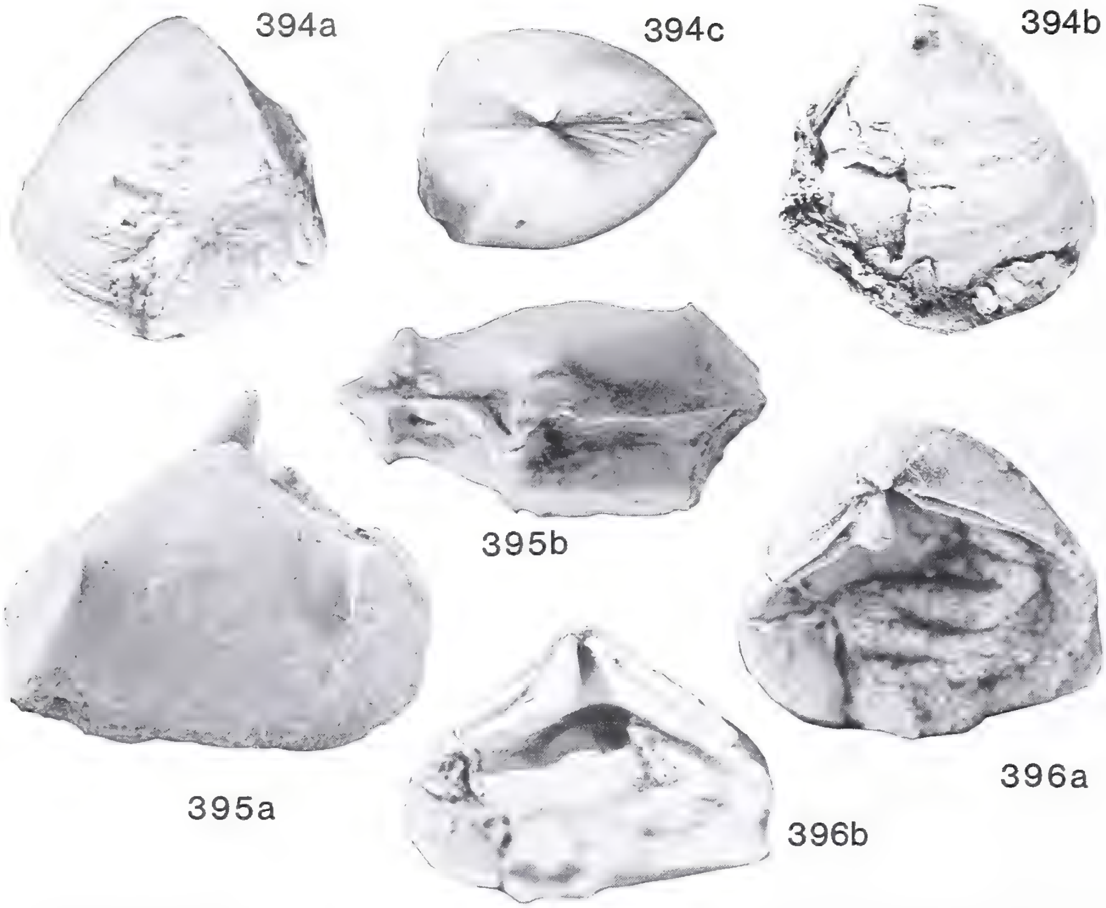
Pachydon hettneri (Anderson, 1928) Figs 394–402

*v 1928 *Corbula hettneri* Anderson: 24; pl. 1, figs 11–14; text-figs 10, 11.
v. 1982 *Anisothyris* sp. Nuttall *in* Bristow & Parodiz: 20.

LECTOTYPE, selected herein: CAS 2698, specimen figured by Anderson, 1928: pl. 1, figs 11, 12 and text-figs 10, 11, 'from near base of Guaduas Group of brackish water beds, near San Juan de Rio Seco'. This locality was originally thought to be Eocene, but is here redated as probably Miocene, Santa Teresa Formation (Porta 1966), possibly located near km 106 on Bogotá–Cambao Highway (Butler 1939, 1942). Downs McCloskey and Thomas Wark colln. Specimen CAS 2699,



Figs 389–393 *Pachydon cuneatus* Conrad. Pebasian. **389**, LL27851; **lectotype** (herein selected) of *Anisothyris tumida* Etheridge, probably figured by Etheridge (1879: pl. 7, fig. 2); Canamá, Peru; Barrington Brown Colln. Left valve, × 2.5. **390**, NYSM 8963; **lectotype** (herein selected) of *Pachydon cuneatus* Conrad, figured by Conrad (1871: pl. 10, fig. 12); Pichana, Peru; Hauxwell Colln. Right valve, × 1.5. **391**, L27725; shell figured as *Anisothyris cuneata* Conrad by Woodward (1871: pl. 5, fig. 8); Pichana, Peru; Hauxwell Colln. a–d, left and right valves, internal and external views, × 2; e, front view, × 2. **392**, **393**, LL28078–9; Puerto Nariño, Colombia; Weeda Colln. Left valves, both × 4.



Figs 394–396 *Pachydon hettneri* (Anderson). ? Miocene, probably Santa Teresa Formation; 'from near San Juan de Rio Seco', near km 106, Cambao to Bogotá Highway, Colombia. **394**, CAS 2698; **lectotype** (herein selected) of *Corbula hettneri* Anderson, figured by Anderson (1928: pl. 1, figs 11, 12; text-figs 10, 11); a–c, left valve, right valve, and dorsal view, all × 3. **395**, CAS 61359a; a, right, and b, dorsal views of internal mould, × 4. **396**, CAS 61359b; a, b, two slightly tilted internal views of dissection of right valve, × 4.

figured by Anderson, 1928: pl. 1, figs 13, 14, and CAS 2700–2705 (unfigured), all from same locality and collection as the lectotype, are paratypes.

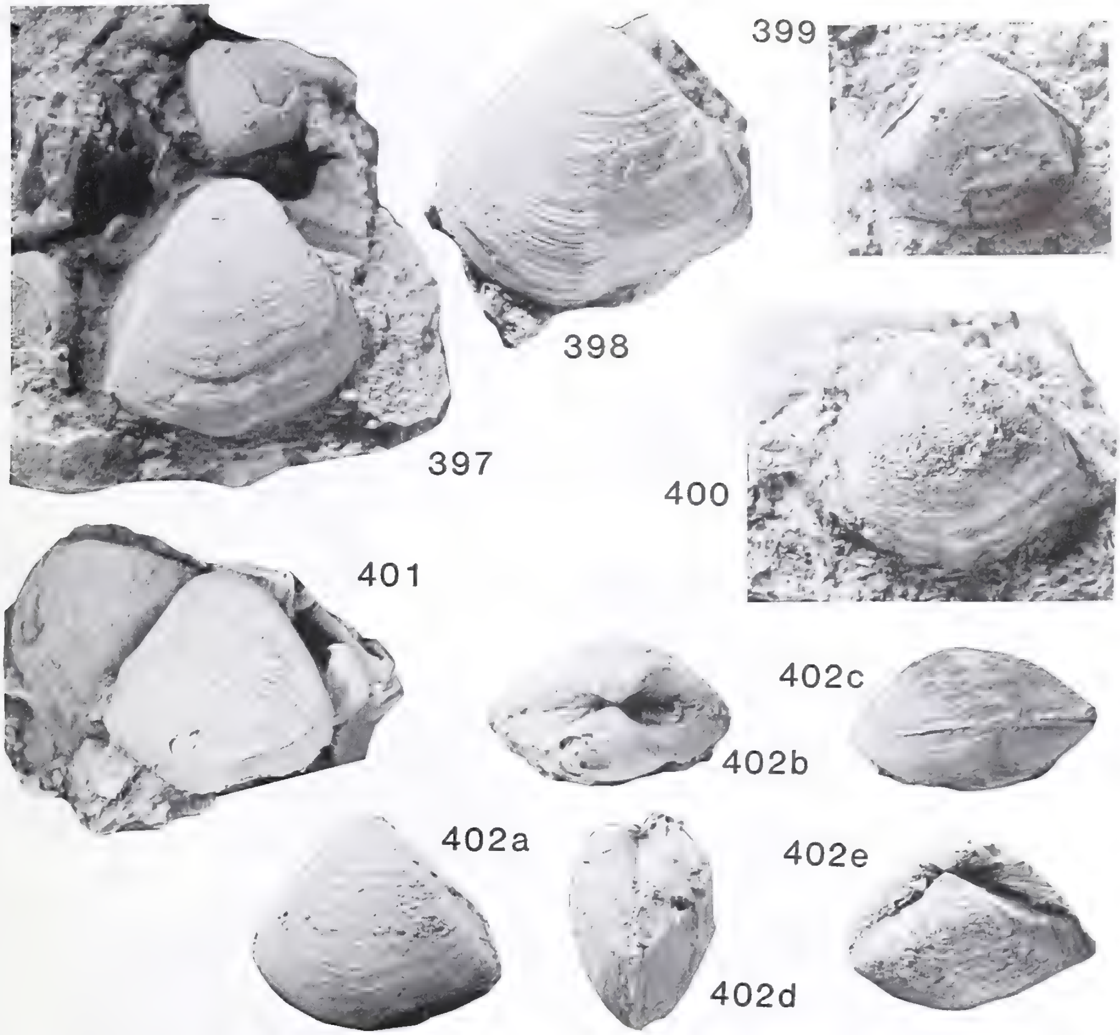
OTHER MATERIAL STUDIED. CAS 31695, more than fifty other specimens from the type locality. These are not regarded as paralectotypes as there is no indication that they were actually studied by Anderson. CAS 61359, two specimens re-registered from CAS 31695 (all same collection as type material). BMPD LL27897–9, LL28086–9, Loc. 33/570–670; LL27884–7, Loc. 33/480–560; LL27903–5, Loc. 33/560; LL4804, Loc. 44; LL4803, Loc. 45; LL27879, Loc. 54; all Late Caenozoic, La Tagua (Eden colln). No further records.

DISTRIBUTION. Santa Teresa Formation and La Tagua Beds, Colombia.

DIAGNOSIS. Tumid, nearly equivalve *Pachydon*; outline equilateral and subtrigonal, often higher than long; umbones at about shell mid-length; corselet broad, extremely truncated, bordered by angular ridge marking maximum breadth of shell.

DESCRIPTION. The anterodorsal and posterodorsal margins of the shell are almost straight in outline, but the ventral margin is evenly rounded. There is a marked flexure at the middle of the ventral margin of some of the La Tagua shells. The umbones are small, in contact, slightly prosogyrous and only moderately incurved. The corselet is clearly differentiated from the flank by an angular ridge, and is divided by a much weaker ridge which is seen commonly in shells from La Tagua, but rarely in the more distorted and less well preserved shells from the Magdalena Valley. In dorsal

DIMENSIONS. In mm.	l	h	br	l/h	br/l
Lectotype, CAS 2698, San Juan de Rio Seco.	14.1	14.6	10.2	0.97	0.72
CAS 2699, figured paralectotype, San Juan de Rio Seco (distorted).	13.1	13.5	–	–	–
LL27903, La Tagua, 33/570–670	8.2	7.2	5.0	1.14	0.61
LL27884, r.v., La Tagua 33/480–560	7.5	7.5	–	1	–
LL27879, l.v., La Tagua Loc. 54	5.5	4.7	–	1.17	–
LL27897/1, r.v., La Tagua 33/570–670	5.2	5.5	–	0.95	–
LL27898, l.v., La Tagua 33/570–670	7.5	7.9	–	0.95	–
LL27897/2, l.v. La Tagua 33/570–670	5.3	5.7	–	0.93	–



Figs 397–402 *Pachydon hettneri* (Anderson). Late Caenozoic; La Tagua, Colombia; Eden Colln; all × 4. **397**, **398**, LL27898, LL27897; Loc. 33/570–670, right and left valves. **399**, LL40804; Loc. 44, latex cast of internal mould of left valve. **400**, LL40803; Loc. 45. **401**, LL27884; Loc. 33/480–560, left valve. **402**, LL27903; Loc. 33/560; a–e, left, dorsal, ventral, rear and oblique view from above left.

view, the posterior of the shell appears almost flattened because the corselets of the two valve meet each other at almost 180°.

The right cardinal tooth lies dorsoventrally. It is fairly large, tear-drop shaped, and pointed dorsally: it is not visible externally. Both the posterior and anterior lateral teeth are strong and lie parallel to the shell margin at the edge of a fairly broad, weakly grooved hinge plate which acts as a socket for the reception of the left valve margin.

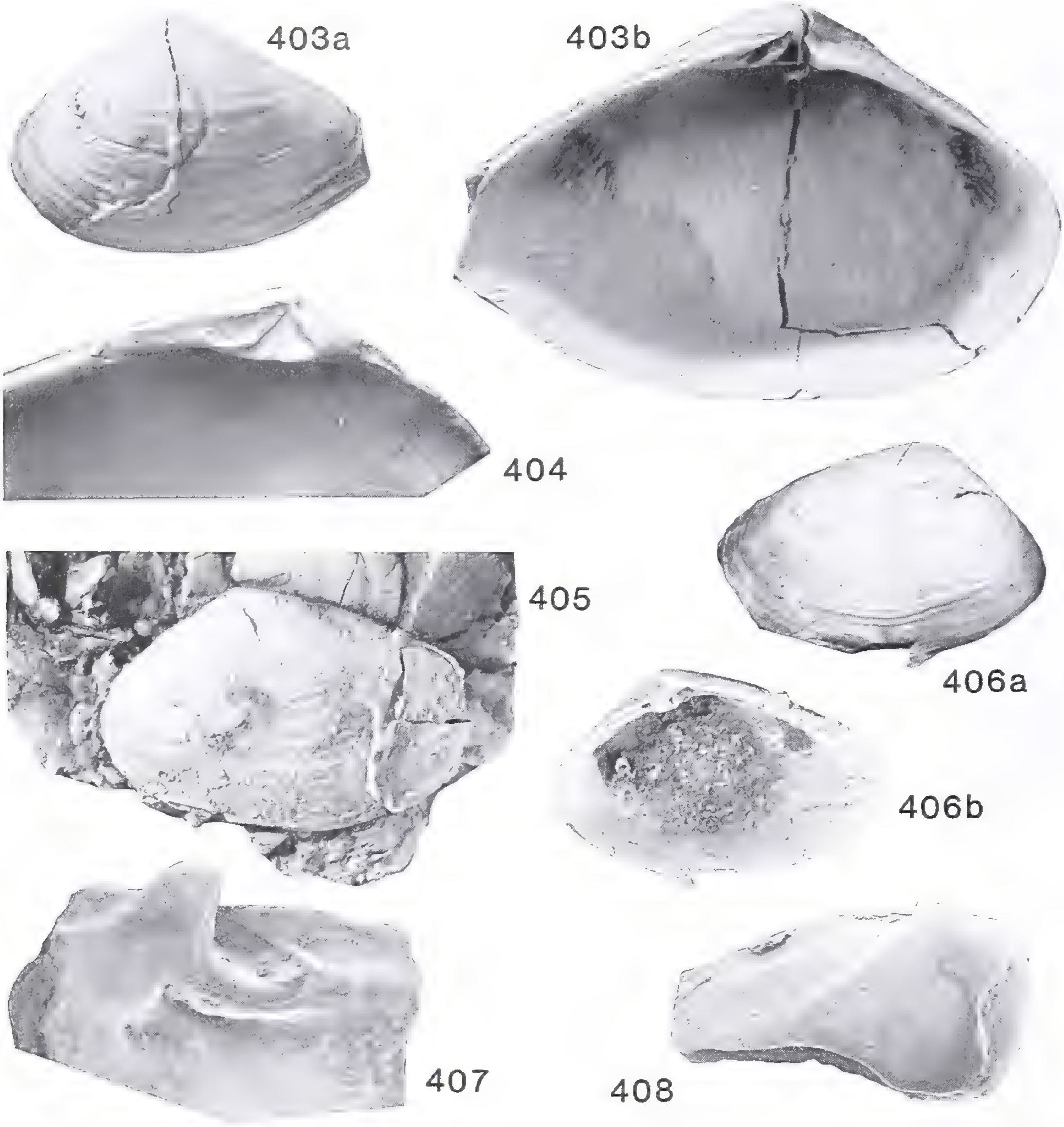
REMARKS. Anderson described both of his figured specimens, CAS 2698 and 2699, as syntypes, and the unfigured ones, CAS 2700–5, as paratypes. The opportunity is therefore now taken to designate CAS 2698, his most complete and least distorted figured specimen, as lectotype. CAS 2699 becomes a paralectotype along with CAS 2700–5. As in the case of *Pachydon cebada* (Anderson), p. 312, described from the same locality, it seems unsafe and unnecessary to regard the numerous specimens from CAS 31695 as paralectotypes.

The specimens from La Tagua are assigned to this species with only slight doubt. They differ in being smaller, and also have the extra minor angulation on the corselet and show flexure in the ventral commissure. The shell surfaces of Anderson's material are too poorly preserved in too coarse a sediment for such features to be seen. A possibly important difference is that the right cardinal tooth in the La Tagua shells appears to be swollen in an anteroventral direction rather than almost dorsoventrally, but unfortunately it has not been possible to reveal all the internal features of specimens from either locality for full comparison.

This species most clearly resembles *P. trigonalis* sp. nov., (p. 309), from Puerto Nariño, which is also almost equilateral, and has a rather similar hinge except that the resilium pit is shallower. It may be distinguished from *P. hettneri* in lacking the prominent corselet and carinate ridge and in being relatively longer.

Pachydon ovalis sp. nov. Figs 403–408

HOLOTYPE. BMPD LL27872, a left valve; late Caenozoic, 1.5 km upstream from La Tagua (Weeda colln). The following



Figs 403–408 *Pachydon ovalis* sp. nov. Late Caenozoic; La Tagua, Colombia. **403**, LL27872, **holotype**, a left valve; 1.5 km upstream from La Tagua; Weeda Colln. a, external, × 3; b, internal, × 5. **404**, LL28092, paratype, left valve; same locality as holotype; internal view, × 10. **405**, LL27881, paratype, left valve; Loc. 33/480–560, × 4. **406**, LL27880, paratype, right valve; Loc 54; Eden Colln. a, external; b, internal, × 4. **407**, LL28094, paratype; from type locality; internal view of right valve fragment showing cardinal tooth and resilium pit on hinge plate with pedal retractor scars below, × 15. **408**, LL28093, paratype; from type locality; fragment of left valve of juvenile specimen, × 10.

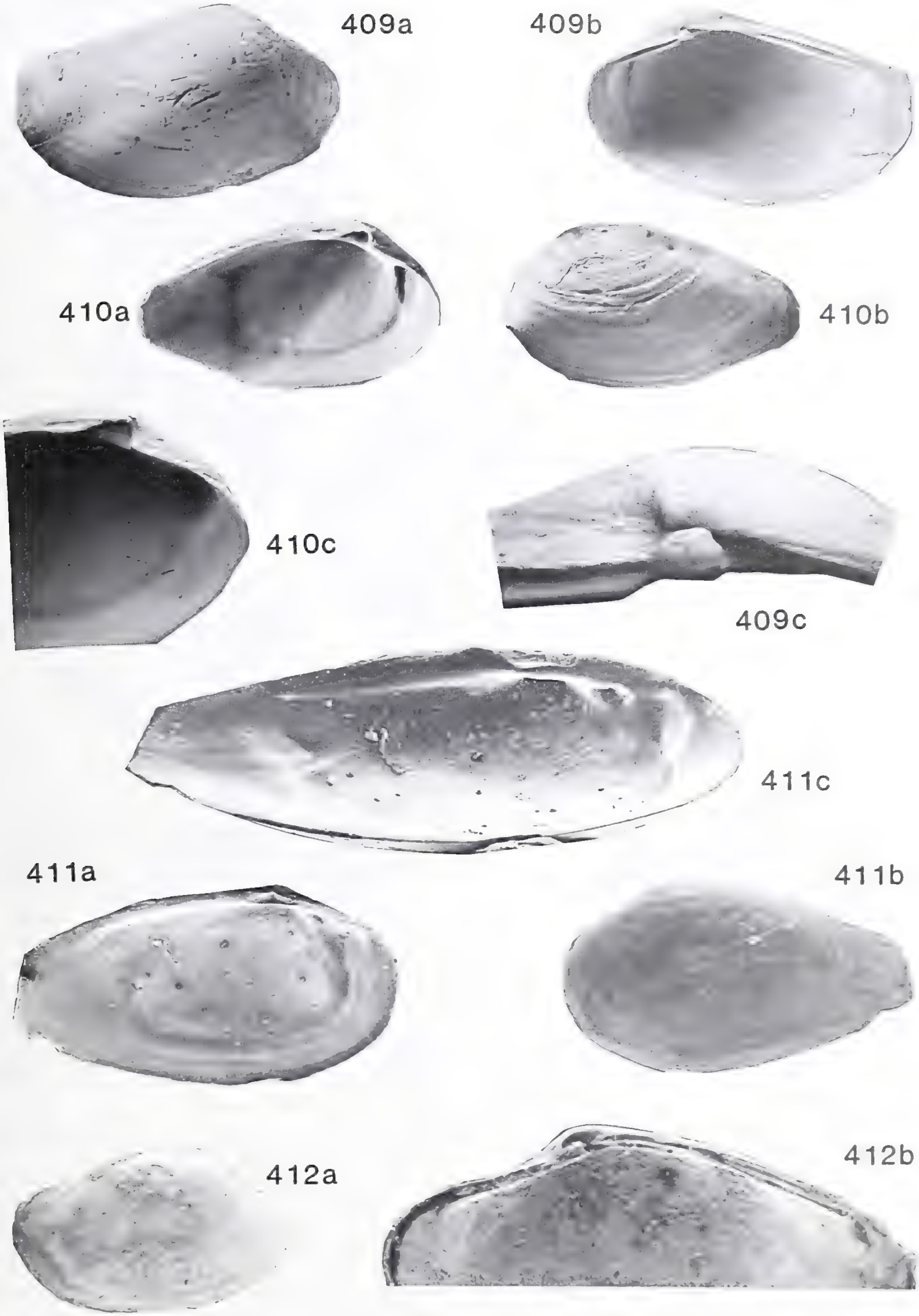
are paratypes; all Late Caenozoic of La Tagua district: LL28090–5, from type locality. Remainder all Eden colln; LL27880, Loc. 54; LL27881–3 (block), Loc. 33/480–560 cm; LL27906 (block), Loc. 33/560 cm.

NAME. 'Egg-shaped, oval.'

DIAGNOSIS. Small, oval, almost equivalve *Pachydon*; umbones not prominent, slightly anterior to mid-length; dentition comparatively weak: pallial sinus deep.

DISTRIBUTION. Late Caenozoic, La Tagua Beds; La Tagua, Colombia, only.

DESCRIPTION. The description is based on single, dissociated valves, but it is clear that the species is virtually equivalve and the ventral commissure shows signs of only a weak flexure. The oval growth lines are modified posterodorsally by a weak, somewhat crassatelliform truncation, but no corselet is differentiated. The slightly prosogyrous umbones are neither prominent nor strongly curved. Internal features of the left valve are known from the holotype, and the paratype LL28092 from the type locality: those of the right valve are known only from paratype LL27880. In this specimen the cardinal tooth is damaged, but appears to lie in a dorsoventral plane. A long anterior lateral tooth lies parallel to and separated from the shell margin by a narrow socket. No true posterior lateral tooth can be seen in this specimen but the posterodorsal shell margin is greatly thickened in the damaged region where a lateral tooth might have been expected. The hinge plate in the left valve is typical of the genus but relatively thin in cross section. Pedal muscle scars are seen just behind the anterior adductor scar, as an anterior extension to the dorsal margin of the posterior adductor scar. Four pits are visible under the hinge plate of paratype


409a
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Figs 409–412 *Pachydon amazonensis* (Gabb). Pebasian; Pichana, Peru; Hauxwell Colln. **409**, LL27907; a, b, right valve external and internal, × 4; c, umbonal area from above, × 15. **410**, LL28062; a, b, left valve, external and internal, × 4; c, cardinal socket, × 6. **411**, LL28064; a, b, left valve, external and internal, × 10; c, inside of valve viewed obliquely from below, × 15. **412**, LL28065, right valve; a, external, × 10; b, internal, × 20.

LL28092. There is a broad, invaginated pallial sinus, stretching from the anterior of the posterior adductor scar half-way to a point below the umbo.

DIMENSIONS. In mm.		l	h	br	l/h	br/l
Holotype, LL27872, 1.5 km upstream from La Tagua	actual	16.0	10.7	4.0	1.54	0.51
	est.	16.5				
Paratype LL27881, La Tagua, 33/480–560		11.2	8.0	–	1.40	–
Paratype LL27880, La Tagua, Loc. 54		11.0	*c.* 7.5	*c.* 2.8	1.47	*c.* 0.51

Note. The above ratios are calculated on estimated dimensions, with shell breadth estimated as twice valve breadth. Other specimens are too fragmentary to measure.

REMARKS. This species is briefly discussed under *P. cebada* (Anderson), p. 312, from which it is distinguished by its more oval, less crassatelliform, outline and its greater size. *P. ovalis* strongly resembles *P. amazonensis* (Gabb). The latter, however, is more elongate, its hinge is lighter and is pallial sinus is a truncation of the pallial line. *P. ovalis* is the only species of *Pachydon* in which such a deep pallial sinus is known, but its other features and its resemblance to *P. amazonensis* suggest that generic separation would be unjustified.

Pachydon amazonensis (Gabb, 1869) Figs 409–412

* 1869 *Tellina amazonensis* Gabb: 198; pl. 16, fig. 4.
. 1878 *Anisothyris amazonensis* (Gabb) Boettger: 499; pl. 13, figs 19a, b, 20a–c, 21a, b.
1924 *Tellina amazonensis* Gabb; Roxo: 44.
. 1938 *Anisothyris amazonensis* (Gabb); de Greve: 30; pl. 6, figs 18, 19; pl. 7, figs 2–4, 7, 8, 10, 11.
? 1966 *Anisothyris amazonensis* (Gabb); Willard: 66–68; pl. 58, figs 4, 5.

TYPE MATERIAL. Gabb's material, described from Pebas, is not listed as being in ANSP (Richards 1968).

MATERIAL STUDIED. BMPD LL27907–9, LL28060–7; Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln, extracted from matrix, 1981).

OCCURRENCES. All Late Caenozoic. Type locality, Pebas, Peru (Gabb 1869, Boettger 1878); Três Unidos, Peru, and Cachoera das Tracoás, Brazil (Roxo 1924); ?Rumi Tuni, Negro Urca and confluence of Rio Mazan and Rio Napo, all Peru (Willard 1966). Late Caenozoic, Pebasian of Upper Amazon Basin only.

DIAGNOSIS. Small, rather tumid, virtually equivalve *Pachydon*; outline resembling *Paphia*, elongate-oval with posterior sometimes truncated.

DESCRIPTION. The elongate-oval shell tapers towards the posterior end, which may be either rounded or truncated and somewhat crassatelliform. The lowest point of the ventral margin is well behind the umbones which are situated between a third and a quarter of the length of the shell from the anterior. The umbones are slightly prosogyrous, low, and not strongly incurved. The right cardinal tooth is hooked, and lies in the plane perpendicular to the hinge line with its anterior surface in contact with the outside world. The resilium pit is subparallel to the dorsal commissure, sloping ventrally at a shallow angle. The anterior adductor scar is strongly pitted and deeply impressed, particularly dorsally. In the right valve LL27907/1, two deep pedal muscle scars are situated side by side just behind the anterior adductor scar. In the best preserved left valve LL27907/2, a single deep pedal muscle scar lies behind the anterior adductor. The postero-dorsal region of the adductor scar is very deeply impressed and may well be a pedal muscle attachment. Two other small muscle scars can be seen, one underneath the posterior end of the hinge plate, and the second just above the posterior adductor scar, which is not strongly impressed. The pallial line is truncated, but not invaginated posteriorly beneath the anterior margin of the posterior adductor scar. Ample space is thus left to accommodate retracted siphons. The commissure is plane except for a weak flexure in the ventral margin.

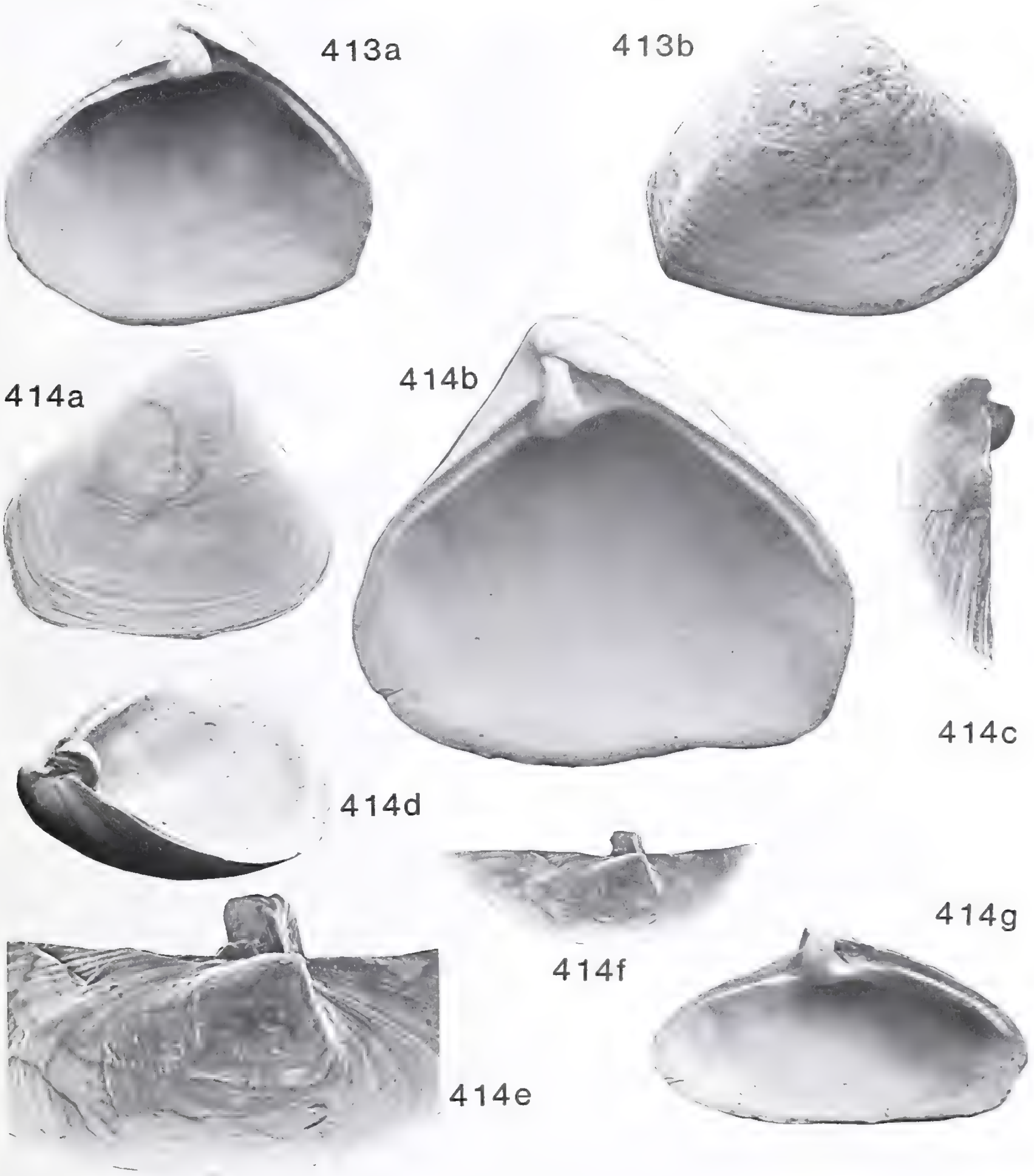
DIMENSIONS. In mm.	l	h	br	l/h	br/l
LL27907/1, r.v., Pichana, Peru	13.1	7.4	3.4	1.77	0.52
LL28062, l.v., Pichana, Peru	11.8	6.6	2.8	1.79	0.48
LL28064, l.v., Pichana, Peru	6.3	3.5	1.3	1.80	0.42
LL28065, r.v., Pichana, Peru	4.3	2.5	1.0	1.72	0.44
PIMUZ 717A, r.v., Iquitos	14.5	7.7	–	1.88	–
Fig'd Boettger 1878: pl. 13, fig. 19; Pebas	4.4	2.3	–	1.90	–
Fig'd Boettger 1878: pl. 13, fig. 20; Pebas	11.5	7.0	–	1.64	–
Fig'd Boettger 1878: pl. 13, fig. 21; Pebas	11.8	6.6	–	1.79	–

Note. Dimensions of Iquitos and Pebas shells calculated from de Greve (1938: pls 6, 7). Breadth measurements are of single valves; br/l ratios take shell breadth to be double valve breadth.

REMARKS. Gabb's type material from Pebas cannot be found in ANSP (Mary A. Garback, ANSP, personal communication). The dimensions he gave were of a small shell (l, 0.25″; 'w', 0.15″; h, single valve, 0.04″) (l, 6.4 mm; h, 3.8 mm; br, 1.0 mm), but he had fragments indicating the presence of a shell twice the size, and his illustration (1869: pl. 16, fig. 4) shows a more elongate shell than his dimensions would suggest (l/h, 1.9 as opposed to 1.7).

The material described by Boettger (1878) came from either Pebas or Pichana and there are no grounds for doubting that the specimens that he figured, which were subsequently refigured by de Greve, are correctly identified. Willard's illustration shows a shell whose outline is not quite typical of the species and whose hinge is not clearly shown. It would appear that the shell might not have been orientated normally for photography, and there must therefore be some doubt about this identification.

For what appears at first to be a small, delicate, species, the shell is surprisingly tumid and the muscle scars remarkably strong. The species is discussed also under *P. cebada* (Anderson), p. 312, and *P. ovalis* sp. nov. (above).



Figs 413–414 *Pachydon trigonalis* sp. nov. Pebasian; Puerto Nariño, Colombia; Weeda Colln; right valves. **413**, LL27860, **holotype**; a, b, external and internal views, × 6. **414**, LL27861, paratype; a, external, × 10; b, internal, × 15; c, front, × 10; d, front oblique view of umbo and cardinal tooth, × 10; e, f, dorsal views showing cardinal tooth, × 40 and × 10; g, internal view obliquely from below, × 10.

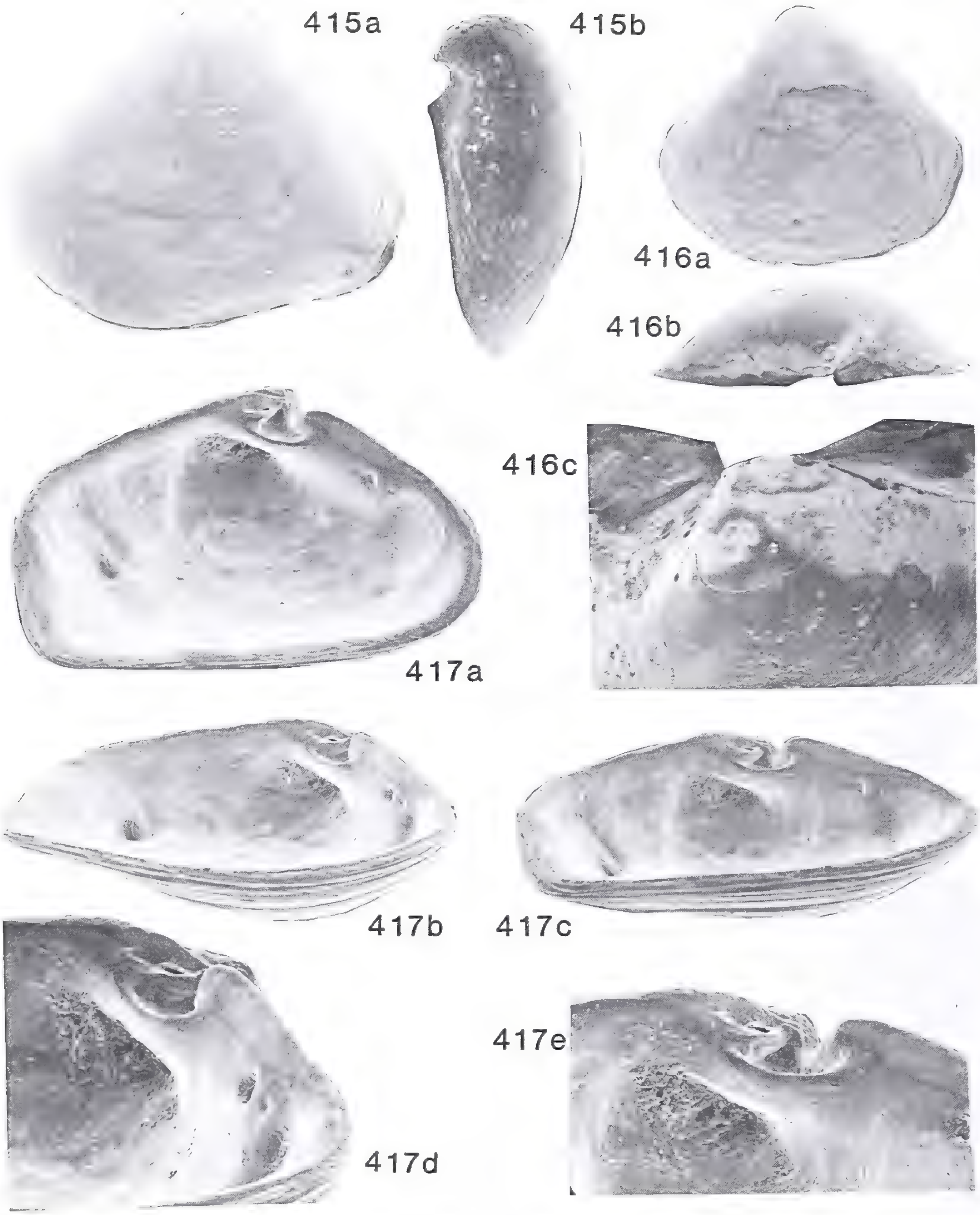
Pachydon trigonalis sp. nov. Figs 413–419

Holotype. A right valve, LL27860; Late Caenozoic; Puerto Nariño, Colombia (Weeda colln). Paratypes LL27861–70, over thirty separate valves and two complete juveniles, locality and horizon as holotype; and LL28007, six juvenile shells, Canamá, extracted in 1984 from matrix of Barrington Brown colln.

Name. 'Triangular'.

Diagnosis. Subtrigonal, crassatelliform in outline, almost equivalve *Pachydon*: umbones erect, at about mid-length.

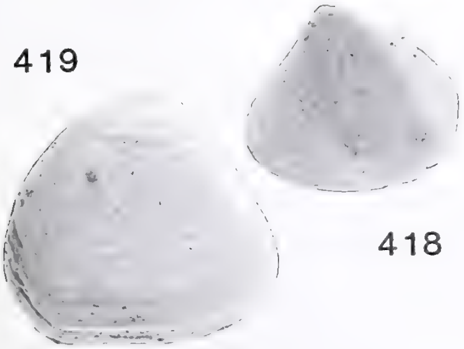
Description. The anterodorsal and posterodorsal margins slope downwards at almost the same angle. The anterior of the shell is well rounded. Posteriorly, a crassatelloid corselet is separated from the flank by a weak, well-rounded ridge. The ridge bordering a region analogous to an escutcheon is also very weak. The ventral margin is barely convex and its deepest point is in front of the umbones. The ventral commissure is also virtually straight and the two valves are of the same convexity. The centrally placed umbones are slightly prosogyrous and touching. The cardinal socket and tooth are comparatively strong but narrow and vertical. The front of the tooth is exposed to the outside world underneath the anterior of the umbones. A shallow pallial sinus is present.



Figs 415–417 *Pachydon trigonalis* sp. nov. Pebasian; Puerto Nariño, Colombia; Weeda Colln; left valves, all paratypes. **415**, LL27862; a, b, external and front views, both × 10. **416**, LL27865; a, b, external and dorsal views, × 10; c, detail of umbonal region, × 40. **417**, LL27863; a–e five internal views; a–c, × 10; d, e, × 20.

DIMENSIONS. In mm.	l	h	br/2	l/h	l/br
LL27860, holotype, r.v., Puerto Nariño.	8.6	7.5	2.7	1.23	1.65
LL27861, r.v., Puerto Nariño.	7.0	6.0	2.3	1.16	1.52
LL27862, l.v., Puerto Nariño.	6.4	5.5	2.0	1.16	1.48
LL28007/1, l.v., Canamá.	3.2	2.9	–	1.10	–
LL28007/2, r.v., Canamá.	3.4	3.1	–	1.10	–

REMARKS. The distinctions between this species and *P. hettneri* (Anderson) are discussed under the latter, p. 305. Both are easily distinguished from other species of *Pachydon* by their trigonal shape. There is some resemblance to *P. erectus* (Conrad), which differs in having more prosogyrous and forwardly positioned umbones and a strongly alate posterior.

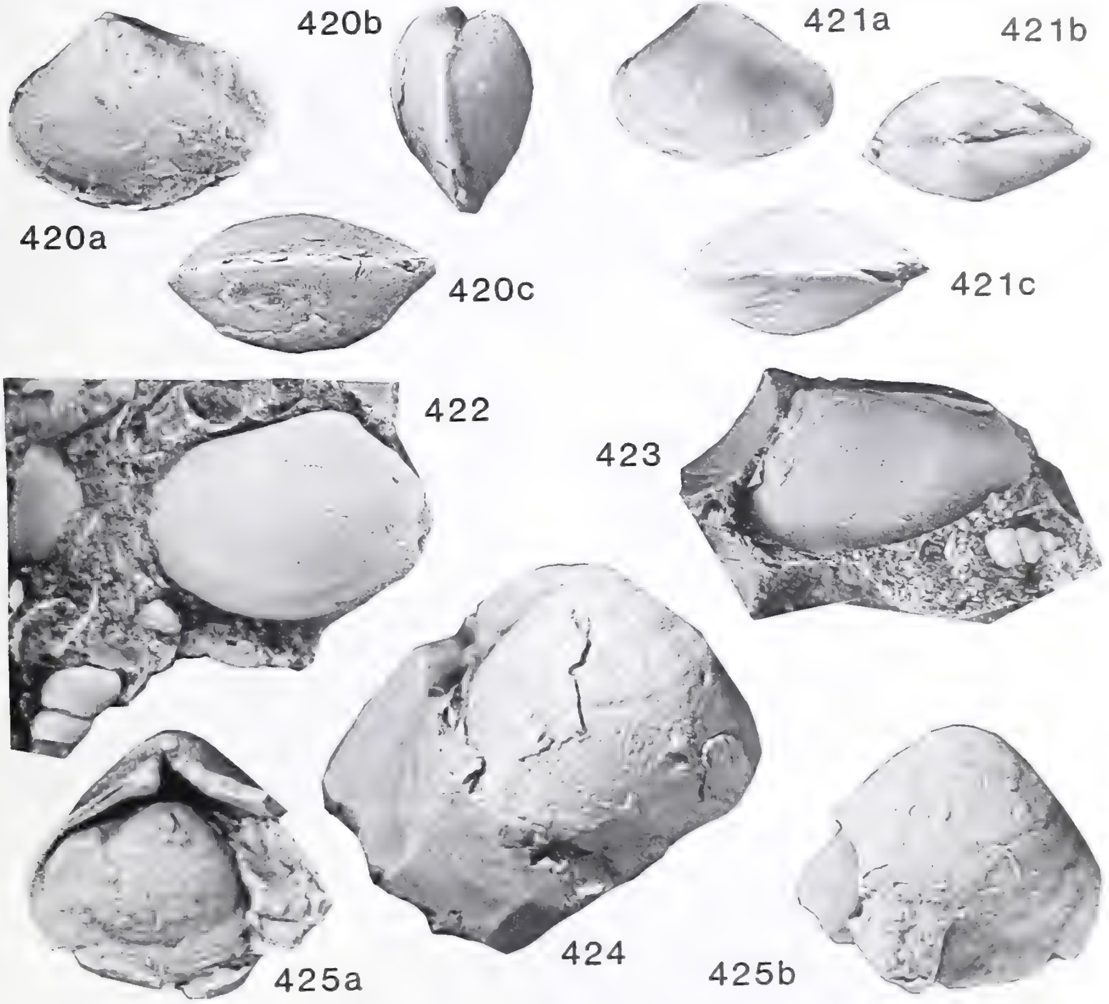


Figs 418–419 *Pachydon trigonalis* sp. nov. Pebasian; Canamá, Peru; Barrington Brown Colln. Paratypes, both × 10. **418**, LL28007/1; left valve. **419**, LL28007/2; right valve.

Pachydon cebada (Anderson, 1928) Figs 420–425

*v 1928 *Corbula cebada* Anderson: 24; pl. 1, fig. 15, text-figs 6, 7.
*v 1928 *Corbula scheibi* Anderson: 25 (*pars*); pl. 1, figs 16, 17 (*non* fig. 18); (*non* text-figs 8, 9).
*v 1935 *Corbula* (*Corbula*) *abundans* Pilsbry & Olsson: 19; pl. 2, figs 13, 14.
*v 1935 *Corbula* (*Erodona* ?) *magdalensis* Pilsbry & Olsson: 20; pl. 4, fig. 8.

HOLOTYPE of *Corbula cebada* (Anderson), CAS 2706, and unfigured paratypes, CAS 2707–14, 'from near San Juan de Rio Seco, eastern border of the Upper Magdalena Valley, Colombia, from near the base of the Guaduas Group, not far above the horizon of the coal veins' (Anderson 1928). Originally dated as Eocene, this locality is here redated as



Figs 420–425 *Pachydon cebada* (Anderson). Probably all Neogene; Colombia. **420**, CAS 2706, holotype of *Corbula cebada* Anderson; figured by Anderson (1928: pl. 1, fig. 15; text–figs 6, 7), probably Santa Teresa Formation; from near San Juan de Rio Seco, probably near km 106, Cambao to Bogotá Highway. a–c, left, front and ventral views, × 5. **421**, ANSP 13077a, **lectotype** (herein selected) of *Corbula abundans* Pilsbry & Olsson; figured by Pilsbry & Olsson (1935: pl. 2, figs 13, 14); Miocene; La Cira Formation, Zopffs, near La Cira, Colombia. a–c, left, dorsal, and ventral views, × 5. **422**, ANSP 13077, previously unfigured paralectotype of *Corbula abundans*, same details as lectotype; right valve, × 8. **423**, ANSP 13075, left valve of the almost entirely decorticated **lectotype** (herein selected) of *Corbula magdalensis* Pilsbry & Olsson, figured by Pilsbry & Olsson (1935: pl. 4, fig. 8), from same locality as *Corbula abundans*; × 5. **424**, CAS 2717, right valve of holotype of *Corbula scheibi* Anderson; same locality as holotye of *C. cebada*; × 5. **425**, CAS 2716, paratype of *C. scheibi* Anderson, same locality as holotype of *C. cebada*; a, b, left and right sides, × 5. (See discussion, p. 312, on unclear original type designations of this species)

Miocene, Santa Teresa Formation (Porta 1966); probably at km 106, Bogotá to Cambao Highway (Butler 1939, 1942) (Downs McCloskey & Thomas Wark colln).

CAS 2716, one of the paratypes of *Corbula scheibi* Anderson, is from the same locality, horizon and collection. See below.

Lectotype, selected herein, of *Corbula abundans* Pilsbry & Olsson, 1935: ANSP 13077a, the specimen originally figured (1935: pl. 2, figs 13, 14). ANSP 13077 is two unfigured paralectotypes. All from Zopffs, near La Cira, middle Magdalena Valley, Colombia; La Cira Formation, originally dated (Pilsbry & Olsson 1935: 8, Wheeler *in* Pilsbry & Olsson 1935: 34–35) as Upper Oligocene or Lower Miocene, but here redated as Miocene.

Lectotype, selected herein, of *Corbula magdalensis* Pilsbry & Olsson, 1935: ANSP 13075, the specimen figured by them (1935: pl. 4, fig. 8), and an unfigured paralectotype on the same block, are from the same locality as *Corbula abundans*. Several other possible paralectotypes are associated with ANSP 13074, on blocks from the same locality bearing the type series of *Potamopyrgus laciranus* Pilsbry & Olsson, 1935, (*Dyris*, herein): see p. 195.

OTHER MATERIAL. CAS 31695, several other specimens of *Corbula cebada* Anderson, in three small samples of grey mudstone from the type locality, have been examined. These are not regarded as paratypes as there is no indication that they were studied by Anderson. The species is further recorded from many other localities near La Cira in the La Cira Formation (Pilsbry & Olsson 1935): not seen. Miocene; Santa Teresa and La Cira Formations, Magdalena Valley, Colombia.

DIAGNOSIS. Small, almost equivalve *Pachydon*; oval with weak crassatelliform corselet developed; umbones slightly anterior to mid-length and not prominent.

DESCRIPTION. The left valve is slightly more tumid than the right. The ventral commissure is curved so as to form a weak central sinus in the left valve. The anterior of the shell is evenly rounded and the posterior is truncated to a varying extent but never strongly. A weak corselet is present; in some shells, however, it can be seen only with difficulty. The slightly prosogyrous umbones are neither prominent nor strongly curved.

Internal features are known from only one specimen, CAS 2716, a paratype of *Corbula scheibi* Anderson, in which part of the right hinge is exposed. It is worn so that neither the exact shape of the cardinal tooth nor the position of the resilifer in relation to the resilium pit can be made out. The anterior of the massive cardinal tooth is exposed to the outside world and slopes at about 45° towards the antero-dorsal commissure, where its base merges with the posterior end of a rather ill-defined elongate anterior lateral tooth. This is separated by a shallow depression from the sharp bordering ridge forming the commissure. The rear margin of the cardinal tooth is cut off vertically by the side of the deep resilium pit. The posterior part of the shell, where a posterior lateral tooth might be expected to lie, is broken away. Muscle scars are not exposed.

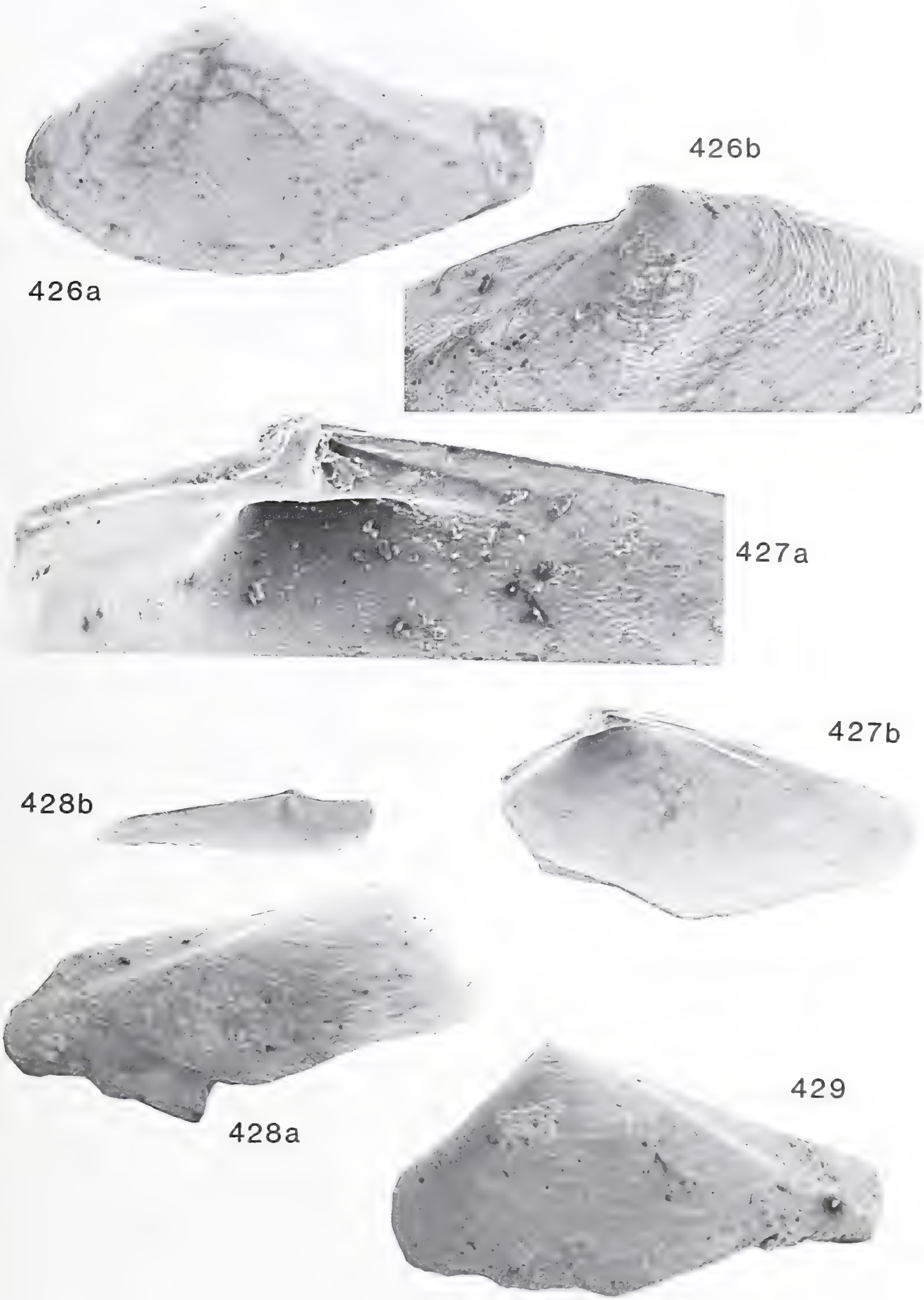
DIMENSIONS. In mm.	l	h	br	l/h	br/l
Holotype of *C. cebada*, Anderson, 1928, CAS 2706, San Juan de Rio Seco.	7.1	5.1	3.6	1.4	0.51
Lectotype of *C. abundans*, Pilsbry & Olsson, 1935, ANSP 13077a, Zopffs.	5.8	3.6	3.0	1.6	0.52
Lectotype of *C. magdalensis*, Pilsbry & Olsson, 1935, ANSP 13075, Zopffs.	7.5(e)	5.0(e)	–	*c*. 1.5	–

REMARKS. *Pachydon hettneri* (Anderson) (p. 302) was described from the same locality as *P. cebada*, and the differences between the two are obvious.

P. abundans and *P. magdalensis* were originally separated by Pilsbry & Olsson (1935) because the latter was crassetelloid in shape and was also described as having the umbones relatively far forward with the posterior part of the shell three times the length of the anterior. The type series of both species come from the same locality (Zopffs), occurring in a hard dark brown mudstone crowded with shells. With the exception of the holotype of *P. abundans*, all are damaged, often partly decorticated and, like the holotype of *P. magdalensis*, partly buried in matrix. In the original illustrations this matrix has been completely blocked out, resulting in a highly distorted representation of the true shape. In fact it would appear that all the shells seen from Zopffs are conspecific. Moreover, the measurements quoted by Pilsbry & Olsson (1935) cannot be reconciled with those now made. However, Pilsbry & Olsson (1935: 20) acknowledged the similarity between their *C. abundans* and *C. cebada* Anderson. They separated the two on the grounds that *C. cebada* had a less plump convex (i.e. right) valve, lacked the concentric wrinkles (greatly accentuated in their heavily retouched type ilustrations) of *C. abundans*, and was larger. But the difference in convexity of valves between the two is slight, and some specimens of *C. cebada* show traces of concentric wrinkling. Furthermore, the size difference seems too slight for specific distinction: the dimensions they quoted for the holotype of *C. cebada* Anderson (length, 6.8 mm; height, 5.3 mm; breadth, 3.7 mm) are also inaccurate: see above.

It is difficult to make a proper assessment of *C. scheibi* Anderson (1928: 25; pl. 1, figs 16–18) from the same locality as *cebada*. In the text and his plate description, Anderson referred to two 'syntypes', CAS 2716 and 2717, as well as paratypes CAS 2718–20. The explanation of his text-figures 8 and 9, however, refers to the 'holotype'. He gave no registration number for it, but the dimensions he quotes show that it can only be CAS 2717, which is also illustrated as his pl. 1, fig. 18. This specimen was subsequently curated at CAS as the holotype of *scheibi* and must be accepted as such, and all the other specimens as paratypes. Unfortunately, CAS 2717 is too badly preserved to be used as a yardstick for the determination of other specimens. The figured paratype CAS 2716 (1928: pl. 1, figs 16, 17) is a rather deformed *C. cebada*, and provides some information on the internal features of that species: see above. None of the other paratypes (CAS 2718–29) are specifically determinable.

P. cebada (Anderson), *P. amazonensis* (Gabb), *P. iquitensis* (de Greve) and *P. ovalis* sp. nov. (p. 305) form a group of small, relatively equivalve, thin-shelled *Pachydon* species with weak umbones. *P. iquitensis* is *Cuspidaria*-shaped with an attenuated and upturned posterior end. *P. amazonensis* from Pebas (Gabb 1869, Boettger 1878, de Greve 1938), Iquitos (de Greve 1938), and Pichana (BMPD, Hauxwell colln) is distinguished by its more forwardly placed umbones, less curved ventral margin, shallower pallial sinus, and by being usually more elongate (l:h usually 1.7–1.9:1, exception-



Figs 426–429 *Pachydon ledaeformis* Dall. Pebasian; Pichana, Peru; Hauxwell Colln. **426**, LL28068; a, left valve, × 15; b, details of umbo, × 50. **427**, LL28071; a, right valve, internal oblique view into umbonal cavity, × 50; b, internal normal view, × 15. **428**, LL28070; a, right valve, × 15; b, dorsal view, × 6. **429**, LL28069; left valve exterior, × 15. Note: LL28069 (Fig. 429) and LL28070 (Fig. 428) were found separately but may well be the two valves of the same individual.

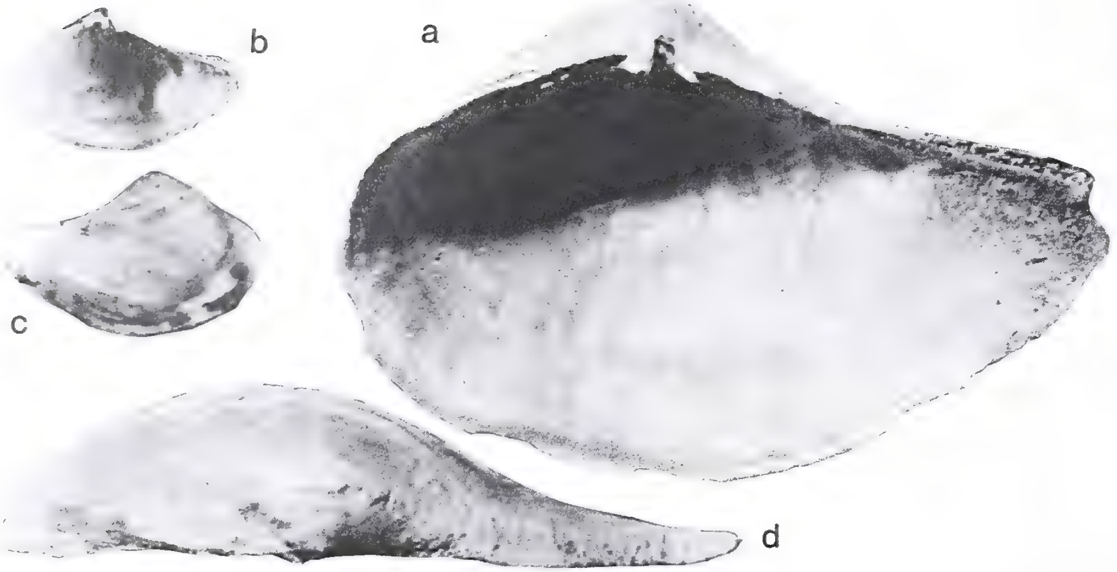


Fig. 430 *Pachydon iquitensis* (de Greve). Pebasian; Iquitos, Peru. Copies of original illustrations of holotype, the only known specimen, a right valve, of *Anisothyris iquitensis* de Greve (1938: pl. 5, figs 38–41). a, internal view, × 6 (fig. 38); b, internal view, × 1.85 (fig. 39); c, external view, × 2 (fig. 40); d, dorsal view, × 6 (fig. 41). Note: de Greve gave no dimensions in his text.

ally 1.4:1; see de Greve, 1938: pl. 7, figs 10, 11, a re-illustration of one of Boettger's Pebas shells).

P. erectus elongatus (Boettger) from Pebas was also refigured by de Greve (1938) and may be readily recognized by its prominent, erect, umbones. The specimen figured by Willard (1966: pl. 56, fig. 3) from 'El Salad', north of Iquitos, as *Corbula abundans* Pilsbry & Olsson is misidentified.

Anderson's trivial name *cebada* is of uncertain meaning, though the Spanish word for 'barley' could be intended. It is taken as a noun is apposition and not an adjective, and therefore not inflected.

Pachydon ledaeformis (Dall, 1872) Figs 426–429

*. 1872 *Corbula (Anisothyris) ledaeformis* Dall: 92; pl. 16, figs 14, 15.

TYPE MATERIAL. USNM, not studied. Upper Amazon Basin, unlocalized, presumed Pebasian (Orton colln, see Remarks).

MATERIAL STUDIED. BMPD LL28068–71, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln, extracted from matrix, 1982).

DIAGNOSIS. Small crassatelliform *Pachydon*; elongate with length about twice height; umbones situated at about one third of length from anterior of shell, posterior rostrate.

DESCRIPTION. The material is fragile and no completely undamaged shell outlines are available in the material at hand. The umbones are not large, but are sufficiently produced to make both the anterodorsal and posterodorsal margins appear slightly concave when the shell is viewed externally. From inside, these margins, which form the two halves of the hinge, appear virtually straight. The shell outline has a slightly truncated, convex anterior, and an almost straight, only slightly convex ventral margin, whilst the posterior of the shell is alate. Careful examination of the growth lines shows that the most posterior point of the shell coincides with the ridge separating the corselet from the main flank of the shell. Damage to all the specimens seen gives the false first impression that the posterior is abruptly truncated. The growth lines, though not strong, are clearly visible and appear to be the same strength on all parts of the shell. The shell is fairly compressed. Although the material consists entirely of dissociated and incomplete valves extracted from washings, it seems that two of them (LL28069, 28070) are likely to be from the same individual: enlarged photographs of the two are exact mirror images. If this deduction is correct, the species appears to be equivalve, apart from the minor differences in the rostrum, and the commissure is straight, or certainly not noticeably curved. The dentition is comparatively light, as in *Pachydon amazonensis* (Gabb), p. 308. Neither muscle scars nor the pallial line can be seen.

DIMENSIONS. In mm.	l	h	l/h
LL28068 (l.v.)	5.8	3.2	1.8
LL28069 (l.v.)	3.9+	–	–
LL28070 (r.v.)	5.2	–	–
LL28071 (r.v.)	4.1+	–	–

Note. The dimensions given by Dall (1872) were: l, 0.3″ (7.6 mm); h, 0.14″ (3.6 mm); this gives a length to height ratio of 2.1.

REMARKS. Dall gave no locality for this species. It was described at the end of a short paper discussing the relationship between Pebasian *Anisothyris* and *Corbula*. Dall stated that it was from Orton's collection. Orton, himself, had collected the material from Pebas described by Gabb (1869), the surviving parts of which are in ANSP. Orton also handled at least part of Hauxwell's collection, which came mainly from Pichana and was divided between several workers (Conrad 1871*a*, *b*, Woodward 1871, and, possibly a later collection, Boettger 1878). The BMPD material was extracted from Hauxwell's collection, mainly from Pichana: on balance, this is the more likely source of Dall's type material, particularly bearing in mind the date of his work and the fact that the Hauxwell collection was almost certainly much larger, and therefore more likely to have been widely distributed, than Orton's own collection.

This species, which Dall thought was the young of an undescribed species, has been neglected since its original description. However, it still cannot be matched with any other known species. *Pachydon erectus elongatus* (Boettger), p. 300, is much more tumid and has a more elongate and well rounded outline. *Pachydon amazonensis* (Gabb), p. 308, is also rather more tumid and lacks any trace of a posterior extension or rostrum.

Pachydon iquitensis (de Greve, 1938) Fig. 430

* 1938 *Anisothyris iquitensis* de Greve: 46; pl. 5, figs 38–41.

Holotype. PIMUZ 394, Pebasian, Iquitos (Peyer colln), a single right valve (not studied). No other material or records.

Dimensions. De Greve gave no measurements. Calculated from his illustrations, however, we have: l, 12 mm; h, 7.8 mm; vbr, 3 mm; umbo situated 5 mm posterior to the most anterior point of shell.

Remarks. This single right valve, which has not been reexamined, was well illustrated by de Greve and clearly merited description as a new species. It is comparatively small for the genus and may be grouped for comparative purposes with *P. amazonensis* (Gabb), *P. cebada* (Anderson), *P. erectus elongatus* (Boettger), *P. ledaeformis* (Dall) and *P. ovalis* sp. nov. (p. 305). Its cuspidariiform outline serves to distinguish it from all but *P. ledaeformis*, which is more elongate and has a corselet bordered by a definite diagonal ridge, whilst *P. erectus elongatus* has a somewhat similar outline but is much more truncated anteriorly. In vertical view, the swollen anterior coupled with the attenuated posterior of the present species give an outline not seen in other species of *Pachydon*.

The single rather poorly preserved specimen, LL27817 (Fig. 451), from the Miocene Loyola Formation of the Cuenca Basin, Ecuador, identified as *? Erodona iquitensis* (de Greve) in Bristow & Parodiz (1982: 31) is here reidentified as *Corbicula (Cyanocyclas) cojitamboensis* Palmer, *in* Liddle & Palmer 1941. This is a very common species in the Cuenca Basin Miocene. This species is not dealt with here as it is discussed in detail and a synonymy given by Bristow & Parodiz (1982: 29, figs 6, 7). LL27817 consists of incomplete internal and external moulds of the anterior end of a left valve of *C. cojitamboensis*. Although there is no clear statement on the subject by Bristow & Parodiz, it would appear that this specimen had erroneously been interpreted as the right valve of a specimen of *P. iquitensis*. This reidentification is of some importance as it eliminates the only record of *Pachydon* from the Neogene of the Cuenca Basin.

Genus ***PEBASIA*** nov.

Type species. *Pachydon* (*Anisorhynchus?*) *dispar* Conrad, 1874*a*. Late Caenozoic, Pebasian; Pebas district, Peru. No other assigned species.

Name. From the locality of Pebas. Feminine.

Diagnosis. Shell very inequivalve, smooth except for growth lines; commissure twisted.

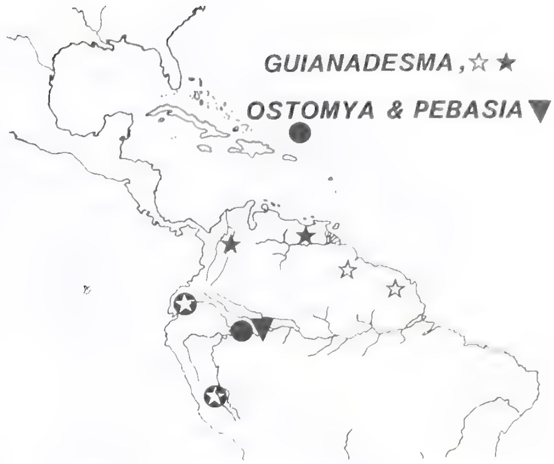


Fig. 431 Neogene and Recent distribution of *Guianadesma* and the extinct genera *Ostomya* and *Pebasia*. ★, Neogene *Guianadesma*; ☆, living *Guianadesma*; ●, Pebasian *Ostomya*; ▼, Pebasian *Pebasia*; ✪, doubtful records of *Ostomya*.

Right valve pholadiform, bilobed, with the two lobes separated by a trough running from umbo to ventral margin; umbo massive, prosogyrous, incurved; right valve hinge similar to that of *Pachydon* with resilium pit lying behind and under massive cardinal tooth and with elongate anterior and posterior lateral teeth lying parallel to commissure.

Left valve twisted, concave, with narrow corselet bounded by angular ridge; triangular area present, resembling that in *Spondylus*; sinus developed in posterior part of area wall to accommodate umbo and possibly also tooth of right valve; socket mounted on inner wall of area, with lanceolate resilifer lying posterior to it as in *Pachydon*.

Muscle scars: posterior adductor scar relatively large; anterior adductor scar lying just ventral to anterior end of area in left valve; in right valve pedal (or byssal) muscle scars situated beside adductors, on side closest to umbo and also just below and in front of umbo; in left valve, scars situated on side of anterior adductor scar closest to umbo and also on middle of area, with a row of pits underneath hinge plate. Pallial sinus shallow.

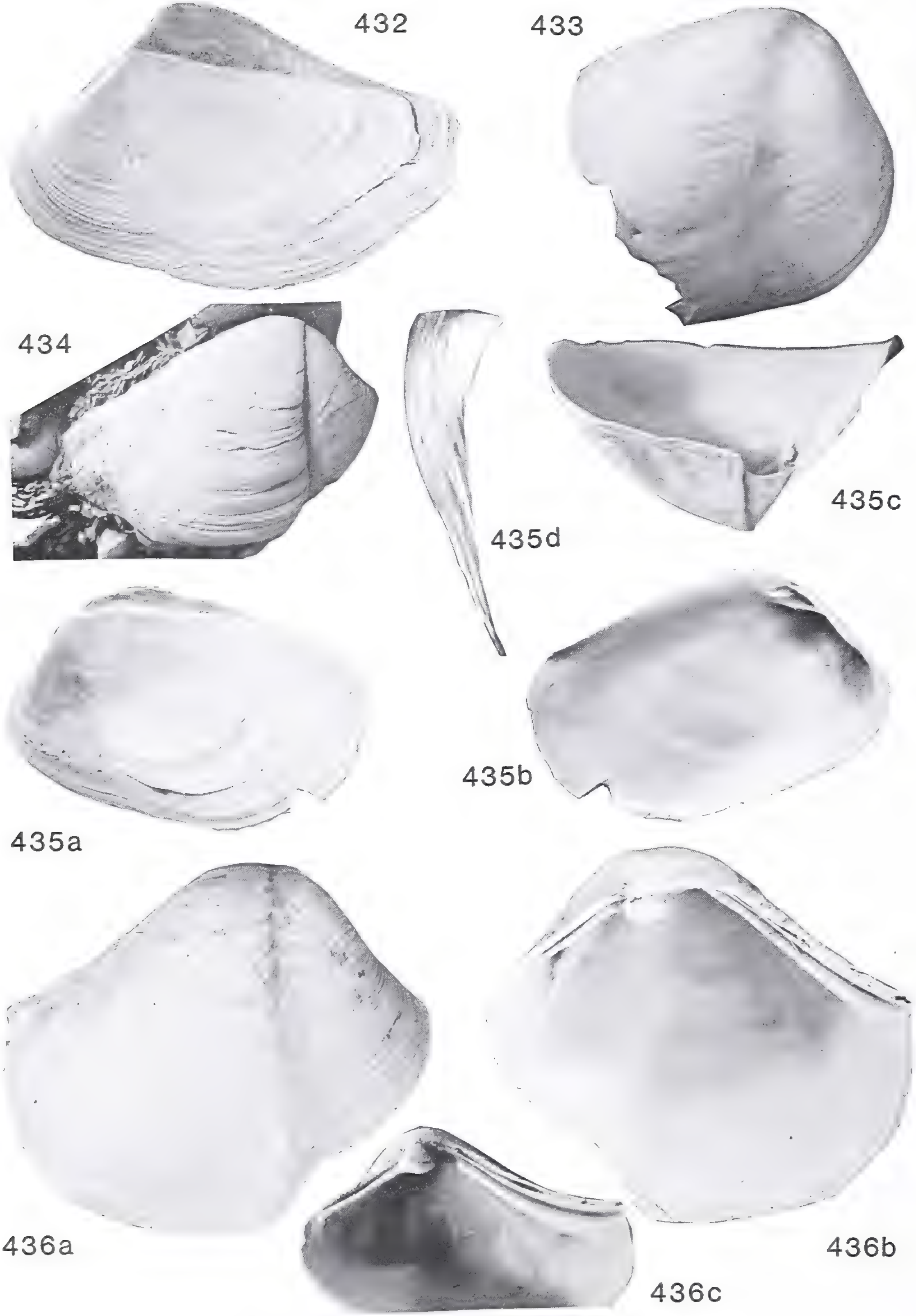
Shell structure: outer layer crossed lamellar; inner layer within pallial line, complex crossed lamellar.

Distribution. Late Caenozoic, Pebasian, of Peruvian and Colombian Upper Amazon.

Remarks. The reasons why the name *Anisorhynchus* is not available for this species have been given already in the discussion on *Pachydon*, p. 292. Pebasia is clearly very similar to *Pachydon* in many respects but is readily distinguished by the *Spondylus*-like area in the left valve. The bilobation of the right valve, though a very obvious feature, seems unlikely to be a fundamental difference. A pedal (or byssal) muscle scar lying under the hinge plate of the right valve is visible in a relatively small specimen of the type species (LL27871); in a larger specimen (LL27953), the scar is invisible because of the greater spiral growth of the valve. No separate pedal (or byssal) scar may be discerned in the region of the posterior left adductor.

Pebasia dispar (Conrad, 1874) Figs 432–436

*v 1874*a* *Pachydon (Anisorhynchus?) dispar* Conrad: 27; pl. 1, fig. 1 (4 figures).



Figs 432–436 *Pebasia dispar* (Conrad). Pebasian; Peru and Colombia. **432**, ANSP 31384, **lectotype** (herein selected) of *Pachydon (Anisorhynchus?) dispar* Conrad, figured by Conrad (1874*a*: pl. 1, fig. 1); either Pebas, Old Pebas or Pichana, Peru; Steere Colln; left valve, × 3. **433**, ANSP 31384, paralectotype, right valve of a different individual, also figured by Conrad (1874*a*: pl. 1, fig. 1), same details as lectotype; × 3. **434**, LL27953; Pichana, Peru; Hauxwell Colln; right valve, × 3. **435**, LL 27910; Pichana, Peru; Hauxwell Colln; left valve; a, external; b, internal; c, rear; d, side view showing concave curvature of outer surface of valve; all × 3. **436**, LL27871; Puerto Nariño, Colombia; Weeda Colln; right valve; a, external, and b, internal views, × 8; c, oblique internal view, × 6.

*. 1938 *Anisorhynchus (?) jeanneti* de Greve: 24; pl. 8, figs 6, 7, 9–17, 20; text-figs 2, 3.

Lectotype (selected herein): ANSP 31384, a left valve. Late Caenozoic, Pebasian; either Pebas, Old Pebas or Pichana (Steere colln). The accompanying right valve of a different individual is a paralectotype.

The type material of *Anisorhynchus (?) jeanneti* de Greve, Late Caenozoic, Pebasian; Iquitos (Peyer colln), in PIMUZ, has not been studied.

Further material studied. All Late Caenozoic, Pebasian. BMPD LL27871, a right valve, Puerto Nariño, Colombia (Weeda colln). LL27910, LL27955, two left valves, and LL27953–4, two right valves, Pichana (Hauxwell colln). LL27935, fragments of both valves, Canamá, extracted in 1984 from matrix of C. Barrington Brown colln (1879). Only recorded from Pebasian, as above.

Diagnosis. As for genus; see p. 315.

Description. In the right valve, the growth lines are flexed in the sinus between the anterior and main 'lobe' of the shell. They are also flexed at the boundary between the corselet and flank. This boundary is a well-rounded fold in adult shells, but in the juvenile (LL27954), it is carinate. The cardinal tooth may increase in size relatively faster than the shell. In the three right valves (BMPD), that of the juvenile is disproportionately small and that of the largest adult is particularly massive. In all specimens, the pallial line is difficult to follow but appears to be simple.

Dimensions. In mm.	l	h	br	l/h
Lectotype, l.v., ANSP 31384	24.2	15.2	–	1.59
Paralectotype, r.v., ANSP 31384	–	17.4	*c.* 8.2	–
LL27910, l.v., Pichana	14.1	9.4	*c.* 2.8	1.5
LL27955, l.v., Pichana	7.9	5.4	–	1.46
LL27953, r.v., Pichana	16.7	11.5	*c.* 5.7	1.45
LL27954, r.v., Pichana (damaged juvenile)	*c.* 2.8	*c.* 1.6	–	–
LL27871, r.v., Puerto Nariño (damaged)	8.8+	7.3	*c.* 2.8	–
PIMUZ 855, l.v., Iquitos, de Greve's measurements (1938: 27)	27.7	14.9	–	1.86
Same shell from de Greve's pl. 8, fig. 9	22.1	14.7	–	1.5
PIMUZ 850, r.v., from de Greve's pl. 8, fig. 12	24.7	17.6	–	1.4

Remarks. Conrad (1874*a*) confused the left and right valves in his description and gave no measurements. He stated that six or seven specimens were before him, including a cast showing both valves in connection. The two shells in sample ANSP 31384 are labelled '? Paratype'. Conrad's illustrations are too poor for either shell to be recognized as being one of those figured. The left valve is here chosen as lectotype because it is the more complete, and the more important characters of the genus are shown by the left valve. De Greve (1938) felt that *P. dispar* was similar but not identical to his new species *Anisorhynchus* (?) *jeanneti*. Examination of material in ANSP and BMPD, in conjunction with de Greve's numerous and informative illustrations, show that the two species are clearly the same. The rather full table of measurements given above suggests that *P. jeanneti* is not relatively more elongate that *P. dispar*.

Although *Pebasia* is somewhat bizarre, it should be measured as a normal dimyarian bivalve, with the length parallel to a line through the adductors: this corresponds with the greatest length. From the orientation of de Greve's figures, he appears to have reached the same conclusion. The species is so inequivalve that the proportions of the two valves are likely to differ: an analogy may be made with the brachial and pedicle valves of brachiopods. Some evidence of this is provided by de Greve: he thought it quite likely that PIMUZ 850 and 855 were right and left valves of the same individual and showed (1938: pl. 8, figs 7, 10 and 17) how well the two fitted together, with the smaller and more elongate left valve fitting into the larger right valve. Checking de Greve's published measurements against his illustrations and scales show, however, that there are some discrepancies. It is clear that the length to height ratio obtained from de Greve's measurements of PIMUZ 855 is too high. The table suggests that this ratio lies between about 1.4 and 1.6 for the species.

All the BMPD shells were recently obtained by breaking down rock matrix with hydrogen peroxide (H_2O_2), and were, therefore, not available for study by Woodward (1871).

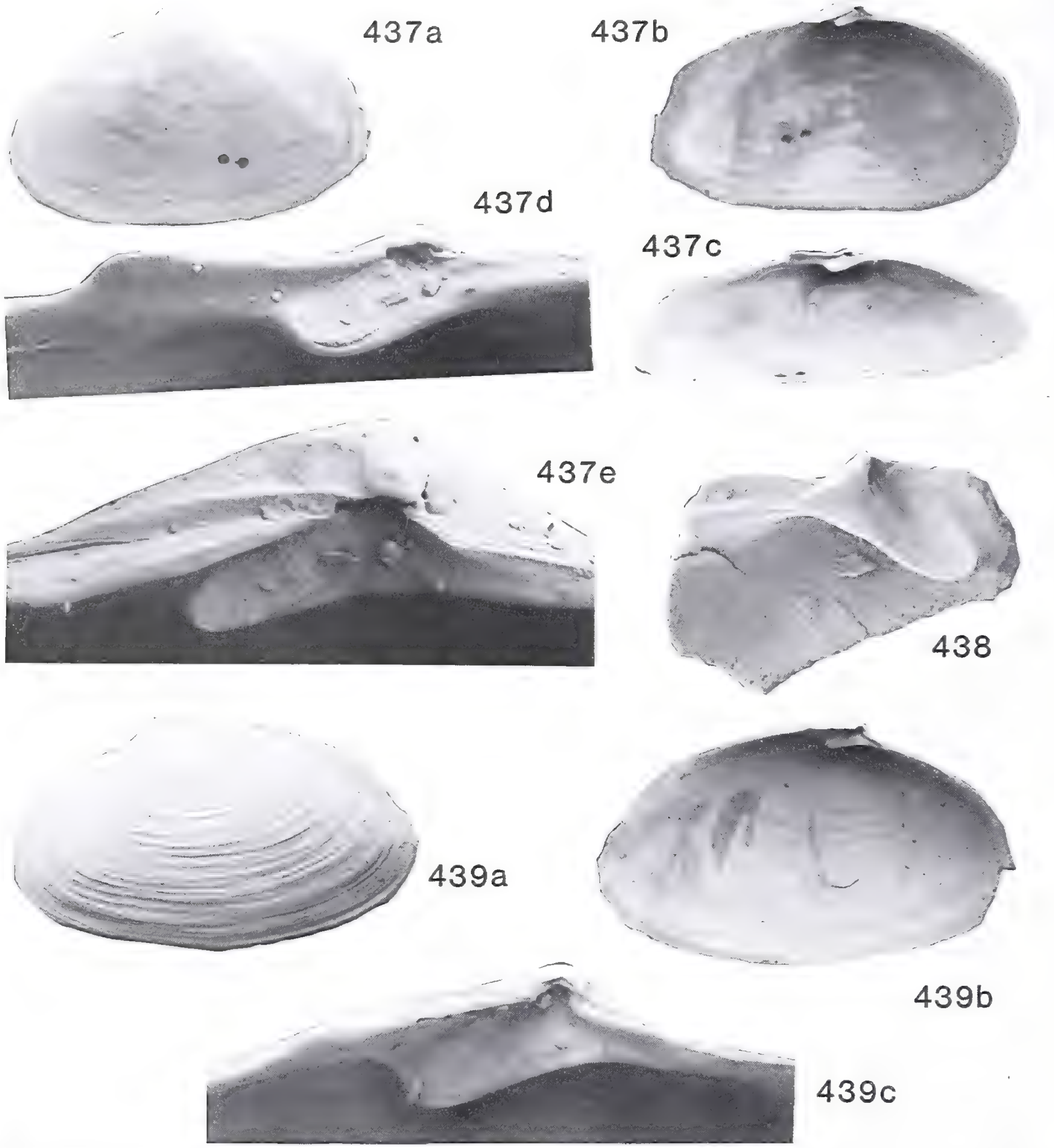
Genus ***OSTOMYA*** Conrad, 1874

Type species. *Ostomya papyria* Conrad, 1874*a*: 30, by monotypy. No other assigned species.

Diagnosis. Small, slender in cross section; outline *Thracia*-like; equivalve or nearly so; thin-shelled, with concentric wrinkles; umbones slightly in front of mid-length, small, pointed, slightly prosogyrous; right valve with angular cardinal tooth of variable strength, apparently with anterior surface not in contact with outside world, sometimes prolonged anteriorly as weak anterior lateral tooth; right valve hinge plate merging posteriorly into thickened platform along dorsal shell margin; resilifers lanceolate, directed posteroventrally at about 45° from hinge line; ligamental nymph of left valve blade-like, perpendicular to commissure; that of right valve lower, considerably thickened; left valve cardinal socket shallow; pallial line obscure, truncated posteriorly, possibly forming shallow sinus; anterior and posterior adductor scars very faint; pedal muscle scars not visible. Shell structure: outer layer crossed lamellar; inner layer, within pallial line, complex crossed lamellar. Nacre absent.

Remarks. The principal differences between *Ostomya* and *Pachydon* are that the former, at any given length, is less tumid, with a lighter, more blade-like cardinal tooth, a shallower cardinal socket and less strongly impressed muscle scars. A comparison with *Guianadesma* is given under the latter, p. 319.

Conrad had described the genus as 'thin, concentrically plicated; hinge with a spoon-shaped oblique fosset in the left valve and a small tooth near the apex; right valve cartilage fosset very oblique, almost parallel with the hinge line.' The resilifers in the BMPD shells described below are not disposed in widely different directions in left and right valves. Unfortunately, owing to the way in which this material was recovered, no paired valves have been identified, with the possible exception of a right valve fragment thought to match left valve LL27917. The right resilifer sinks below the level of the commissure more than that in the left valve and is more strongly buttressed from below. This is perhaps what Conrad meant.



Figs 437–439 *Ostomya papyria* Conrad. Pebasian; Pichana, Peru; Hauxwell Colln. **437**, LL27916; left valve; a–c, external, internal and oblique internal views, all × 8; d, e, two views of umbonal region showing nymph and resilifer, both × 40. **438**, LL27922; fragment of right valve showing cardinal tooth and resilifer, × 10. **439**, LL27917; left valve; a, external, and b, internal views, both × 8; c, umbonal region, × 40.

Ostomya is known only by its type species: other fossil species previously assigned to it are now removed. *O. colombiana* Pilsbry & Olsson (1935) is transferred to *Guianadesma* and *O. mencheri* Palmer (1945) is placed in synonymy of *G. sinuosum* Morrison (1943), p. 319. Pilsbry (1944) described two poorly preserved species from a single locality in the Red Beds of the Pachitea River, Peru as *O. terminalis* and *O. pachiteana*. Their hinges are unknown. *O. terminalis* might be referable to *Pachydon*, but I am unable to suggest a genus for *O. pachiteana*, though it does not appear to belong to either *Ostomya* or *Guianadesma*.

Ostomya papyria Conrad, 1874 Figs 437–439

. 1874*a* *Ostomya papyria* Conrad: 30; pl. 1, figs 6.
? 1879 *Thracia* sp., Etheridge: 84.
? 1879 *Lutraria* sp., Etheridge: 84.
. 1969 *Ostomya papyria* Conrad; Keen *in* Moore: N847 (*pars*); fig. F24.5

TYPE MATERIAL. Not seen. There is no record of the types in ANSP (Richards 1968).

MATERIAL STUDIED. All Late Caenozoic, Pebasian: BMPD LL27916, complete left valve; LL27917, a complete left valve with the umbo of a right valve, thought to be the same individual; LL27922, fragment of right valve. LL27918–21, ten fragmentary left and right valves; all Pichana, Peru, Hauxwell colln, 1870, extracted 1981. LL27923–5, three left valve fragments; LL27926–9, eight right valve fragments; LL27930, two shell fragments lacking umbones; all Puerto Nariño, Colombia, Weeda colln.

FURTHER RECORDS. Late Caenozoic, Pebasian; either Pebas, Old Pebas or Pichana (Conrad 1874*a*); ? Canamá (Etheridge, 1879). Pebasian only, Upper Amazon Basin of Peru and Colombia.

DIAGNOSIS. As for genus; see p. 317.

DESCRIPTION. The two left valves, LL27916–7, are moderately compressed, the flank and corselet being separated by a weak posterior angulation in one shell but not the other. The ventral commissures of both are slightly twisted. The shell surface is concentrically wrinkled and the growth lines are closely spaced and rugose. No radial sculpture is present. The umbonal regions of the broken right valves show similar concentric sculpture. These wrinkles appear to be frequently obliterated in worn specimens, giving the false impression that spacing between them is a variable feature. Larger shell fragments (LL27930) show irregular, non-commarginal wrinkling at the extremities of the shell. The dorsal margin is raised both anterior to the umbo and also immediately posterior to it over the nymph, producing a slightly auriculate effect. In the left valve, a pit-like socket is gouged into, and sometimes even through, the umbo of the valve, slightly truncating the anterior end of the resilifer. The resilifer is bordered posterodorsally by a weak ridge with a socket above it. The commissure operates as a weak lateral tooth immediately anterior to the umbones. In the right valve also, a pit-like socket invades the umbones. A tooth of variable shape and strength lies anterior to the umbones. It is basically similar to that found in *Pachydon*, but less massive and peg-like. It is frequently prolonged forwards as an anterolateral tooth lying parallel to the dorsal margin, from which it is separated by an elongated socket. The pallial line is obscure but appears to be truncated or weakly sinuate posteriorly. Both the anterior adductor and the posterior adductor, which has a large posterior retractor scar lying above and in front of it, are only just visible.

DIMENSIONS. In mm.	l	h	br	l/h
LL27916, l.v., Pichana.	6.2	3.7	*c.* 1.0	1.68
LL27917, l.v., Pichana.	7.0	4.2	*c.* 1.0	1.67

REMARKS. Although no complete valves have been found at Puerto Nariño, the growth lines indicate that the shells from both this locality and Pichana are very similar. No other small species remotely resembling Conrad's figures have been found in any of our washings. This suggests that these specimens can only belong to Conrad's species, and they are all here assigned to *O. papyria*. It is impossible to make an accurate estimate of valve size from fragmentary material of this type. It is probable that the largest shells from Puerto Nariño were about 20 mm long and 10 mm in height, but it seems unlikely that any of the shells from Pichana would have exceeded 15 mm in length.

It is possible that the records of the marine genera *Thracia* and *Lutraria* from Canamá (Etheridge 1879) are in reality *Ostomya*: they are tentatively added to the synonymy.

Genus ***GUIANADESMA*** Morrison, 1943

[? = *Anticorbula* Dall, 1898: 839, *nom. nov.* pro *Himella* Adams, 1860: 203 (*non* Dallas, 1852, Insecta), type species *Himella fluviatilis* Adams, 1860: 203 (*nom. dub.*) by monotypy; Recent, ? Marañón River, Peru.]

TYPE SPECIES. *Guianadesma sinuosum* Morrison, 1943; Recent, Guyana.

DIAGNOSIS. Elongate kidney-shaped in outline; umbones well forward, low, prosogyrous; fairly tumid in cross section; slightly inequivalve with left valve dorsal margin resting inside margin of right valve and posteroventral margin of left valve lying within right valve; commissure with strongly twisted ventral margin; periostracum wrinkled; edentulous; resilifers lanceolate, that of left valve lying parallel to plane of commissure on weak hinge plate, that of right valve lying in groove underneath thickened dorsal shell margin and facing ventrally; ligamental attachments lying along dorsal commissure behind umbones, that in left valve directed dorsally, that in right valve directed ventrally; muscle scars irregularly shaped, two pedal/byssal muscle scars lying on line between anterior adductor and umbo; posterior pedal/byssal retractor muscle scar large, joined to anterodorsal side of posterior adductor scar; pallial sinus shallow. 'Byssus present; foot, short, cylindrical; mantle largely fused with foot and byssal opening and opening for the two short separate siphons, with a briefly continued internal septum; inner and outer branchiae subequal, eulamellibranchiate, free below from the abdominal sac and from the mantle' (Morrison 1943). Shell structure: outer layer, crossed lamellar; inner layer, within pallial line, complex crossed lamellar. Nacre absent.

OTHER SPECIES ASSIGNED. *Ostomya colombiana* Pilsbry & Olsson, 1935: 21; Miocene, La Cira Formation; Magdalena Valley, northern Colombia.

GENERIC DISTRIBUTION. Neogene, northern South America. Recent, rivers in the Guyanas, in brackish and possibly fresh water.

REMARKS. In the above diagnosis, the features of the soft parts are largely quoted from Morrison (1943), but characters of the shell are those observed in BMZD specimens and, as pointed out on p. 290, Morrison's reference to the shell being nacreous-porcellanous cannot be supported. *Guianadesma* differs from *Ostomya* in being more irregularly shaped with tumid, ingrown umbones, and with a strong flexure in the ventral commissure of the right valve. Its resilifers are more elongate and lie nearly parallel to the hinge, but at markedly different attitudes in the two valves. Its nymphs and hinge plate are relatively lighter and it is edentulous.

Guianadesma sinuosum Morrison, 1943 Figs 440–442

* 1943 *Guianadesma sinuosum* Morrison: 49; pl. 8, figs 1–6.
. 1944 *Ostomya fluviatilis* (H. Adams) Pilsbry: 147; pl. 11, figs 42–44; text-figs 1a, b.
*. 1945 *Ostomya mencheri* Palmer: 21; pl. 2, figs 1–7.
. 1968 *Anticorbula sinuosa* (Morrison) Altena: 156, 176.
. 1969 *Anticorbula sinuosa* (Morrison); Altena: 26, 28, 29, 43.
v. 1971 *Anticorbula sinuosa* (Morrison); Altena: 82; pl. 10, figs 15, 16 (*cum syn.*).

HOLOTYPE (of *Guianadesma sinuosum* Morrison), USNM 53691, living; rocks midstream of Cuyuni River, opposite Kartabo Point, near junction with Mazaruni River, Essequibo

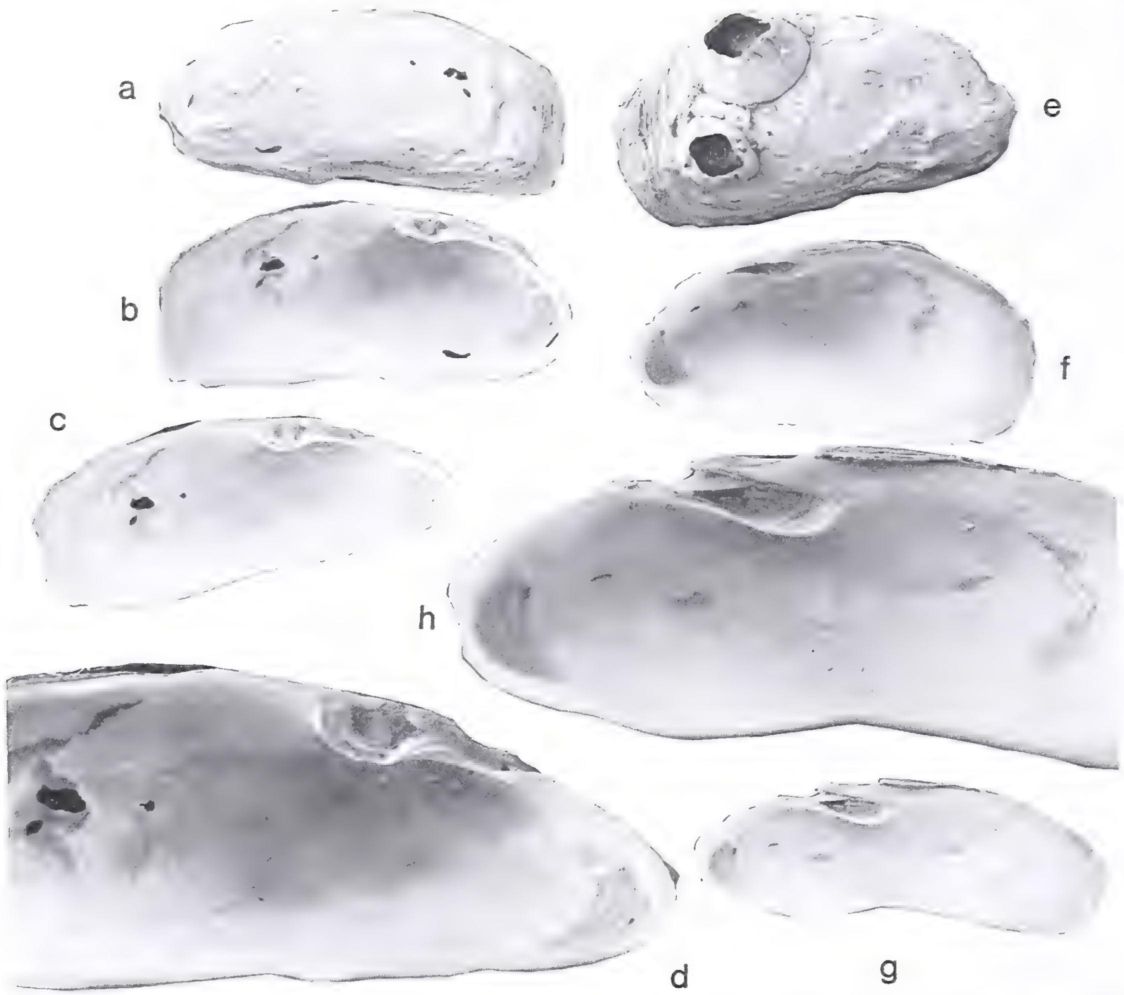


Fig. 440 *Guianadesma sinuosum* Morrison. Recent; Surinam, Maroni (Marowijne) River between Langamankondre and Christiaankondre. BMZD 1984228; pres'd Dr C.O. van Regteren Altena. a–d, all left valve; a, external, × 2.5; b, internal, × 2.5; c, d, internal tilted, × 2.5, × 5. e–h, all right valve; e, external showing barnacles in life position, × 2.5; f, internal, × 2.5; g, h, internal tilted, × 2.5, × 5.

District, Guyana (Morrison colln). Not studied. Paratypes, in USNM and Carnegie Museum, Pittsburgh (Morrison and J. Benkert collns).

MATERIAL STUDIED. Six shells, BMZD 1984228; banks of Marowijne River between Langamankondre and Christiaankondre, Surinam (Altena colln). This would appear to correspond with Locs 95–96 from where Altena (1971: 83 and map, pl. 11) records the species collected live. In his full locality list (1969: 41), however, Christiaankondre is given as Loc. 94 and Langamankondre as Loc. 95.

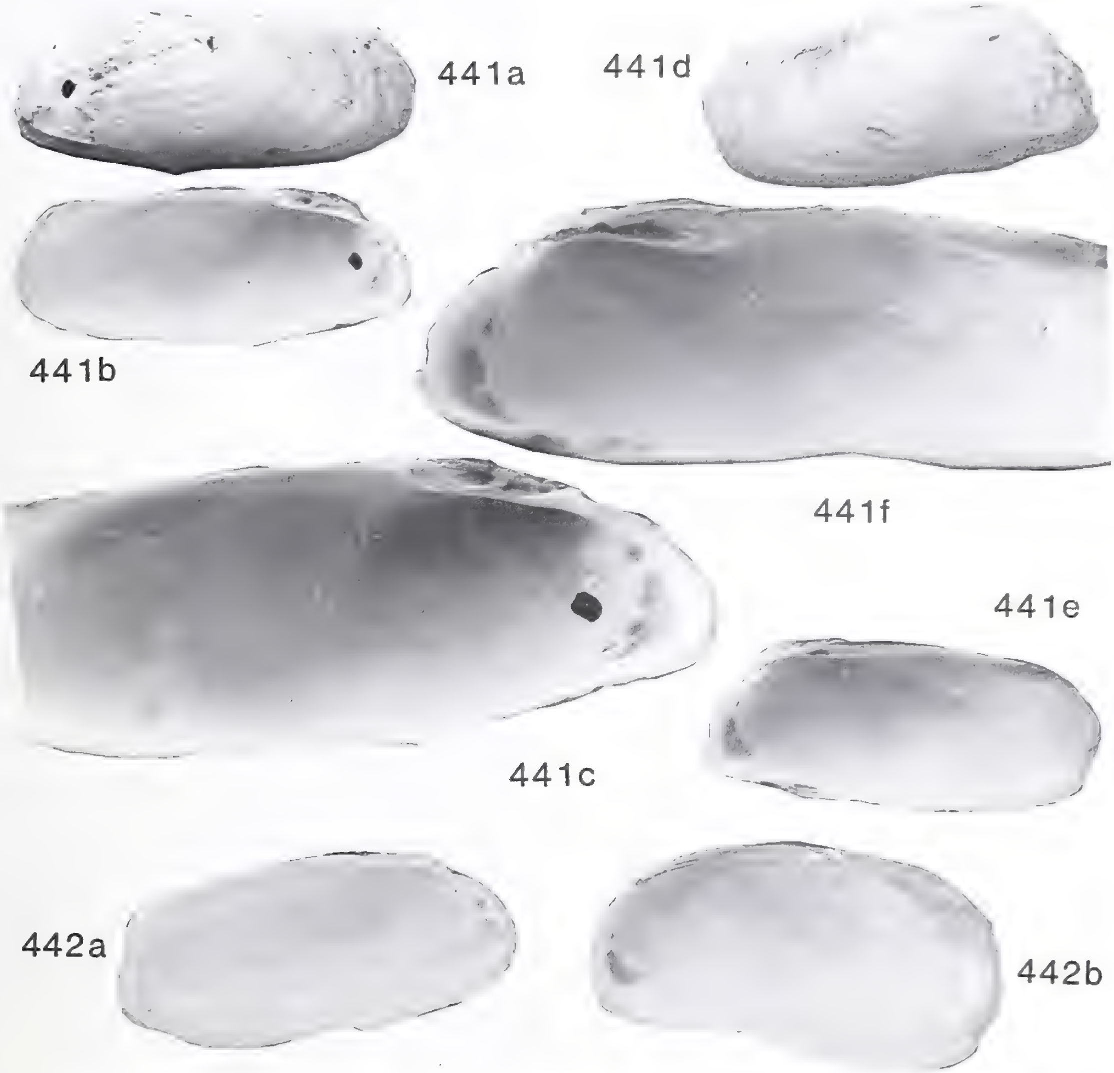
FURTHER DISTRIBUTION. 'Plio-Pleistocene', La Llanera, State of Monogas, Venezuela (Palmer 1945, as *O. mencheri*). Recent, Cuyuni River, Guyana (Morrison 1943); numerous localities, particularly Surinam and Marowijne Rivers, Surinam (Altena 1968, 1969, 1971); washed ashore, Marowijne River, French Guiana (Altena 1971).

DIAGNOSIS. As for genus; see p. 319.

DESCRIPTION. The shape of the shell, including the length to height ratio and the extent to which the posteroventral margin of the right valve overlaps that of the left, is variable. The anterior point of the shell is low down and the anterior adductor is placed almost as far forward as is possible. The outline of the shell is kidney-shaped with a concave ventral

DIMENSIONS. In mm.		l	h	br	l/h
Holotype, USNM 53691. Cuyuni River, Guiana.	l.v.	17.4	9.8	7.0	1.77
	r.v.	17.3	11.1		1.56
Marowijne River, Surinam. Altena 1971: pl. 10, fig. 16	l.v.	24.9	12.3	–	2.02
Marowijne River, Surinam. Altena 1971: pl. 10, fig. 15	l.v.	25.4	12.3	–	2.03
BMZD 1984228, Marowijne River, Surinam (Altena colln).	l.v.	20.8	8.7	8.1	2.39
	r.v.	20.8	9.1		2.28
BMZD 1984228, Marowijne River, Surinam (Altena colln).	l.v.	20.8	9.5	6.8	2.19
	r.v.	21.2	10.9		1.90
'Marañon River', no scale given. Pilsbury 1944: pl. 11, fig. 43	r.v.	–	–	–	1.81
'Marañon River', no scale given. Pilsbury 1944: pl. 11, fig. 43 (different specimen)	l.v.	–	–	–	1.70
Holotype of *Ostomya mencheri* Palmer, 1944, PRI 20084.	l.v.	20	11	8	1.8
Paratype of *O. mencheri* Palmer, 1944, PRI 20087.	r.v.	20	12	8	1.67
Himella fluviatilis, from H. Adams, 1860, 'Rio Marañon'.	–	21.2	12.7	8.5	1.67

Note. Adams' measurements are converted from l, 10 lines; h, 6 lines; br, 4 lines, at 12 lines = 1 inch (1 line = 2.12 mm). Breadths are of both valves together.



Figs 441–442 *Guianadesma sinuosum* Morrison. Recent; Surinam. BMZD 1984228; same locality and collection as Fig. 440. **441**, a–c, all left valve; a, external, × 2.5; b, c, internal, × 2.5, × 5. d–f, all right valve; d, external, × 2.5; e, f, internal, × 2.5, × 5. **442**, a, b, left and right valves, internal views, × 2.5.

margin. The ventral commissure is flexed, more strongly in the right valve than in the left. In all the BMZD specimens the umbones are badly eroded. In some cases other areas have been worn to such an extent that holes have appeared in the shell. The periostracum is concentrically wrinkled, particularly anteriorly, whilst posterior to the flexure it is formed into numerous radiating rib-like thickenings. Concentric and radiating elements form a net-like pattern over much of the shell surface. This is confined to the periostracum: there is no evidence that the patterning extends to the calcareous shell which is unsculptured except for slightly rugose growth lines.

REMARKS. Morrison collected the holotype, USNM 53691, live from rocks in midstream of the Cuyuni River, opposite Kartabo Point, near the junction with the Mazaruni River, Essequibo District, Guyana in July, 1925. He stated (1943: 50) that paratypes were present both in USNM and Carnegie Museum, Pittsburgh. The species was moderately abundant, byssally attached to igneous rocks and gravel in the river current, but absent from rocks surrounded by mud bars (1943: 51).

Altena (1969: 29; 1971: 83) reported finding the species sometimes byssally attached in old borings of teredinids in the Surinam River. The strong flexure of the ventral commissure and the rather modioliform shell outline with a concavity in the ventral margin are entirely in keeping with a byssally attached mode of life, and it is possible that the more elongate, *Lithophaga*-like individuals are those which lived in tubes. The overlap of the two valves is best illustrated by Morrison (1943: pl. 8, fig. 4) – a ventral view – and by Altena (1971: pl. 10, fig. 16) – a view of a left valve with its dorsal margin lying below that of the right valve and showing the larger posteroventral region of the right valve. Because hinge teeth are lacking, the articulation and fit of the two valves depends on the ligament, internal resilium and the way in which the commissures overlap in the region below and just anterior to the umbones. It is difficult to reconstruct the articulation accurately either with the dissociated valves available in BMZD or with fossil material (Palmer 1945: pl. 2, figs 1–7), which is sometimes distorted.

The eroded umbones of even the smallest shell, 6.8 mm long, in BMZD, and the worn appearance of the periostracum seen in all published photographs (Morrison 1943, Palmer 1945, Altena 1971) suggest that at least a fairly high proportion of shell damage occurs during life. This would be consistent with a byssally attached epifaunal existence in river currents. Unfortunately, it has not been possible to examine specimens positively known to have lived in teredinid borings, but the most elongate and least inequivalve specimens in BMZD are the least worn. The illustrations of the shells identified by Pilsbry as *Ostomya fluviatilis* (H. Adams), and also those of *O. mencheri* Palmer, show that they fall within the range of variation of shell-shape exhibited by the well-localized material from the Guianas, and are here placed in synonymy. Palmer had also distinguished her species from *G. sinuosum* because it lacked radial striations. It is now known, however, that this is merely a feature of the periostracum and not the shell.

Ostomya colombiana Pilsbry & Olsson, 1935, was described as being rather like *O. fluviatilis* in shape. The type illustration is a drawing, partly reconstructed, of a left valve 6.7 mm long. No particular features distinguish it from *G. sinuosum* except that the umbo seems to be noticeably more swollen.

Opinions about the salinity tolerance of *G. sinuosum* have changed. Morrison (1943: 51) collected the species from the Cuyuni River with the fresh-water *Doryssa consolidata* (Bruguière). Altena (1969: 24–29) drew attention to the great changes in salinity produced by seasonal variation in rainfall in the Surinam River from which he recorded *G. sinuosum*. It is of interest to note that Morrison's collection was made in July 1925, just after the peak of the wet season and corresponding with the period of lowest salinity. Two of the specimens which Altena presented to BMZD, and which came from the region of his Locs 94–96, between 5 and 15 km from the mouth of the Marowijne River where it is about 5 km wide, are encrusted with barnacles. The positioning of the barnacles, near the posterior of the shells and externally, suggests that they were present while the bivalves were alive. Both the presence of the barnacles and the proximity of open sea show that *G. sinuosum* can live in fairly high salinities. In his series of papers, Altena developed the idea that different groups of species characterized different salinities, though acknowledging that the picture could change with further collecting. He eventually found the downstream limit of *G. sinuosum* (1971: 83) overlapping the upstream limit (1975: 12) of the mainly estuarine *Neritina zebra* (Bruguière). Earlier (1969: 26, 28) he had reported that their ranges did not overlap. This proven co-occurrence of *Guianadesma* and *Neritina* is perhaps analogous to the *Pachydon+Neritina* association in rich Pebasian faunas.

REVIEW OF OTHER FOSSIL FAUNAS

Pebas, Peru

Orton Collection 1867, described by Gabb, 1869

Professor James Orton of Vassar College, New York State, spent a few hours on 12 December 1867 collecting at Pebas, which was in those days described as a small village on Rio Ambayacú, one or two miles (1.6–3.2 km) from where it flows into Rio Marañón, some 50 or 60 miles below the mouth of Rio Napo. This was the first collection of fossils to be made from the Pebas Beds, and is of special importance for another reason. Orton collected only from Pebas, and there is therefore no doubt about the locality from which his fossils came. The fossils were described by Gabb and are in ANSP. Gabb (1869: 197) wrote that the locality was a high bluff at Pebas, on the Ambayacú, two miles above its confluence with the Marañón.

The Pebas fauna described by Gabb, 1869:

original determinations	**revised determinations**
Neritina pupa (Linné)	*Neritina ortoni* Conrad
Turbonilla MINUSCULA Gabb v	*Liris minuscula* (Gabb)
Mesalia ORTONI Gabb	*Dyris ortoni* (Gabb)
Tellina AMAZONENSIS Gabb	*Pachydon amazonensis* (Gabb)
PACHYDON OBLIQUA Gabb	*Pachydon obliquus* Gabb
Pachydon TENUA Gabb	*Pachydon tenuis* Gabb

[In this, and in subsequent lists, new taxa are given in capital letters; 'v' indicates that original specimens have been studied by me.]

This collection, though small, shows the unusual character of the 'Pebasian' fauna. It contains no elements of the present-day Amazonian fresh-water fauna. *Neritina* ranges from the intertidal zone into fresh-water streams, but is typically never found far from a shore line. *Pachydon* is an extinct genus allied to *Corbula* and may be regarded as being virtually diagnostic of these 'Pebasian' faunas. Corbulidae are essentially marine, though the related Erodonidae tend more to be found in brackish waters.

Orton's material is of particular importance, not only for historical reasons, but also because it is one of the few early collections with clear-cut locality data. Shortly afterwards Juan Hauxwell, an English traveller who spent about thirty years in Amazonia, made fossil collections predominantly from another locality, Pichana, but mixed with a few fossils from Pebas. Hauxwell's collections were described by both Conrad (1871*a*, *b*) and by Woodward (1871). Steere's collection described by Conrad (1874*a*) was a mixture of fossils from both of these localities and also from a third site, Old Pebas.

Hauxwell Collection, date unknown, described by Boettger, 1878

The fossils described by Boettger (1878) were collected by Hauxwell at some unknown date. Kadolsky (1980: 365) regarded it as probably a third fraction of the collection from Pichana and Pebas described independently by both Conrad and Woodward in 1871. However, he informed me (personal communication) that Boettger's specimens of *Eubora crassilabra* (Conrad) and *E. bella semisculpta* (Boettger) in the Senckenburg Museum, Frankfurt (SMF) are both labelled 'Pebas'. Moreover, Boettger (1878: 486) in his introduction wrote about the Conrad/Woodward collection as though it were entirely separate. He referred to it as coming from two localities near Pebas on the south side of Rio Marañón, i.e. the opposite side (right bank) of the river from Pebas. The mention of two localities is probably due to the fact that Pichana was also referred to as Cochaquinas (in error). Boettger then went on to discuss the relationship between Pebas 'lying on the left (i.e. East) bank of Rio Ambayacú one English mile above its junction with Rio Maranon' and Old Pebas 'lying two English miles below the mouth of Rio Ambayacú'. Finally (1878: 488–9) Boettger discussed the collection which he, himself, was describing. He stated that

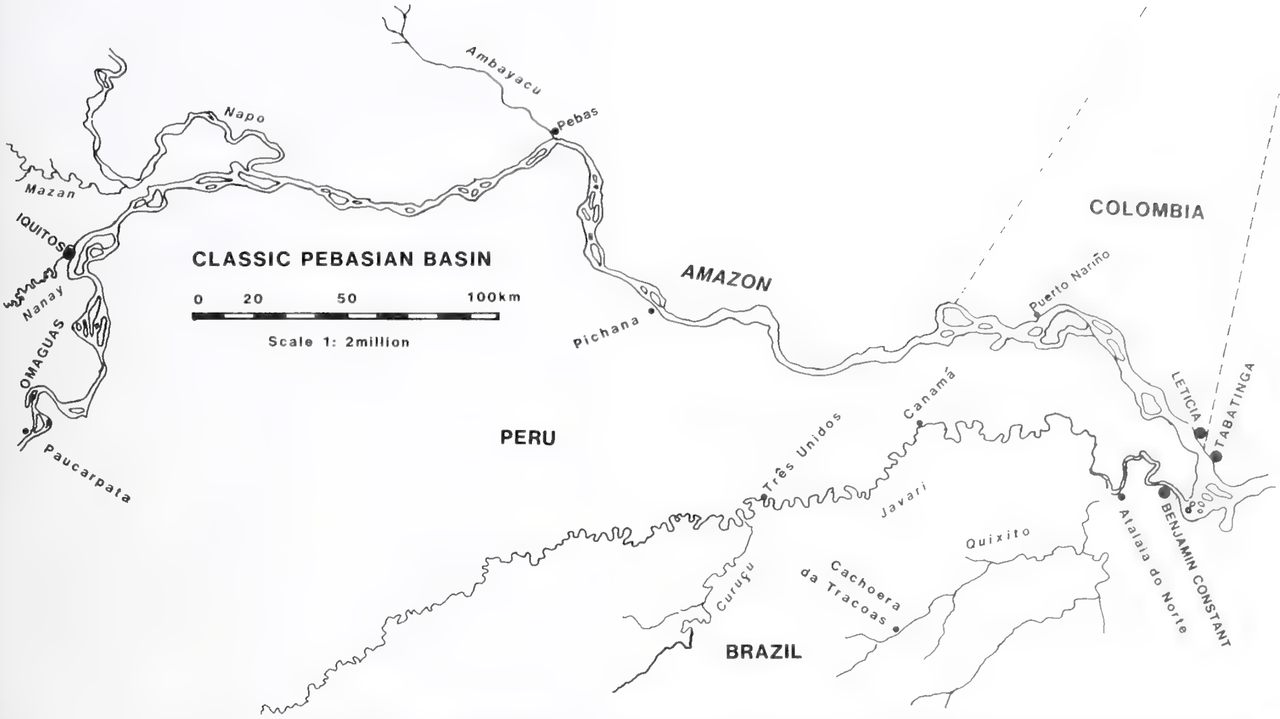

Ambayacu
Pebas
Napo
Mazan
IQUITOS
Nanay
OMAGUAS
Paucarpata
CLASSIC PEBASIAN BASIN
0 20 50 100km
Scale 1: 2million
AMAZON
Pichana
COLOMBIA
Puerto Nariño
LETICIA
TABATINGA
PERU
Canamá
Três Unidos
Javari
Quixito
Cachoera da Tracoas
Curuçu
BRAZIL
Atalaia do Norte
BENJAMIN CONSTANT

Fig. 443 Classic Pebasian Basin. To show the new locality of Puerto Nariño and the classic localities of the Pebasian Basin of easternmost Peru, and neighbouring areas of Brazil and Colombia.

he owed his material to the kindness of Dr W. Kobelt of Schwannheim, who, in turn, had received it from Herr R. Abendroth of Leipzig in 1877. A letter from the last-named gentleman which accompanied the fossils mentioned that the village of Pebas was 'forty miles above the Brazilian frontier fort of Tabatinga . . . The fossils came from a blue clay at one place near the town . . . Abendroth's fossils came from Mr Hauxwell, an Englishman, who spent several years in the region . . .'

Thus, the arguments as to whether or not all Boettger's material came from Pebas itself are fairly evenly balanced. He was clearly aware of the presence of the other localities and hence of the possible confusion. On the other hand, part of Abendroth's letter read like a translation into German of the description of Pebas and its relation to Tabatinga given in Hartt (1872). This raises the suspicion that this letter was not based on first-hand observations by the collector Hauxwell. Hauxwell certainly had the time to revisit Pebas. Boettger's fauna has much in common with those described by Conrad and Woodward mainly from Pichana. The true Pebas fauna so far known is very small and the fossils were said (Orton, *in* Conrad 1871*b*) to be more common at Pichana. However, Orton's visit to Pebas was, in any case, so short that he may well not have done that locality justice.

The bulk of the collection is in Senckenburg Museum, Frankfurt, and has not been studied herein. The holotype of *Pseudolacuna macroptera* Boettger was refigured by Cossmann (1915) and is now in Université de Paris (Kadolsky, 1980: 372–373), who refigured it. Kadolsky also refigured (1980: fig. 10) the holotype of *Eubora bella semisculpta* (Boettger). Several of Boettger's specimens were refigured by de Greve (1938): details are noted in the Iquitos faunal list given here (p. 332). Species not figured by Boettger are indicated by '(no fig.)' in the list below.

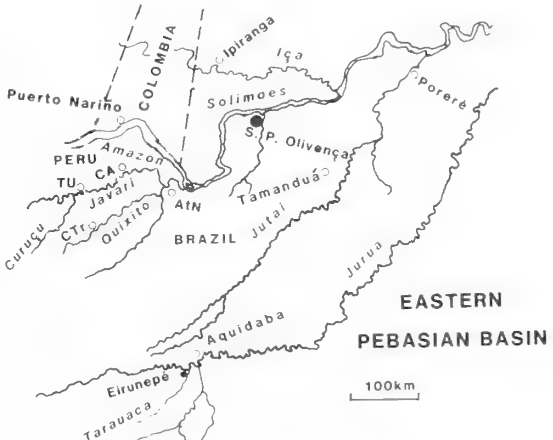

COLOMBIA
Ipiranga
Içá
Poreré
Puerto Nariño
Solimoes
S.P. Olivença
PERU
Amazon
CA
TU
Javari
Tamanduá
AtN
Curuçu
CTr
Quixito
BRAZIL
Jutai
Juruá
EASTERN PEBASIAN BASIN
Aquidaba
Eirunepé
Tarauacá
100km

Fig. 444 Eastern Pebasian Basin. Showing the localities of the easternmost part of the Pebasian Basin, lying immediately to the east of the classic area outlined in Fig. 443. Details of most Brazilian localities are based on maps and text in Fernandes *et al.* (1977) and del'Arco *et al.* (1977). All localities shown have yielded Pebasian faunas except for Aquidaba, which has yielded a fauna very like that of the present-day Amazon. Several fossil mammal localities lie adjacent to Rio Jutai. No Pebasian molluscs have been recorded from them. Abbreviations: **AtN**, Atalaia do Norte; **CA**, Canamá; **CTr**, Cachoero de Tracoas; **TU**, Três Unidos. Localities marked as rings, towns as black circles.

original determinations	**revised determinations**
Bulimus linteus Conrad (juveniles only, no fig.)	*Orthalicus linteus* (Conrad)
Neritina ortoni Conrad	*Neritina ortoni* Conrad
Hydrobia (Isaea) ortoni Gabb (no fig.)	*Dyris ortoni* (Gabb)

original determinations	revised determinations
Hydrobia (Isaea) CONFUSA Boettger	*Dyris ortoni* (Gabb)
Hydrobia (Isaea) TRICARINATA Boettger	*Dyris tricarinata* (Boettger)
Hydrobia (Isaea) gracilis (Conrad) (no fig., fragments only)	*Dyris gracilis* Conrad
Lacuna (Ebora) crassilabris (Conrad)	*Eubora crassilabris* (Conrad)
Lacuna (Ebora) bella (Conrad)	*Eubora bella* (Conrad)
Lacuna (Ebora) bella var. *semisculpta* Boettger	*Eubora bella* (Conrad)
PSEUDOLACUNA MACROPTERA Boettger	*Toxosoma eborea* Conrad
Turbonilla minuscula Gabb	*Liris minuscula* (Gabb)
Dreissena FRAGILIS Boettger	*Mytilopsis* sp. (? *scripta* (Conrad) and/or *sallei* (Recluz)
Anodonta batesi (Woodward) (no fig.)	?*Anodontites* sp. (fragments)
Unio sp. (no fig.)	unionid, ?*Diplodon* (fragments)
Anisothyris amazonensis (Gabb)	*Pachydon amazonensis* (Gabb)
Anisothyris tenuis (Gabb)	*Pachydon tenuis* Gabb
Anisothyris cuneata (Conrad)	*Pachydon cuneatus* Conrad
Anisothyris erecta (Conrad)	*Pachydon erectus* Conrad
Anisothyris erecta (Conrad) var. *ELONGATA* Boettger	*Pachydon erectus elongatus* (Boettger)
Anisothyris obliqua (Gabb)	*Pachydon obliquus* Gabb
Anisothyris carinata (Conrad)	*Pachydon carinatus* (Conrad)

Boettger also recorded the following non-molluscan taxa: *Serpula* sp., *Percidarum* sp., *Rajidum* sp.

Boettger listed both (1878: 493) *Hydrobia (Isaea) lintea* Conrad (=*Dyris lintea*) and (1878: 496) *Hemisinus sulcatus* Conrad (=*H. brasiliensis*), specifically mentioning that neither was present in his material.

This fauna of sixteen named molluscan species (if *Mytilopsis* is included), is very similar to that found in the parts of Hauxwell's collection revised herein and described by both Conrad (1871*b*) and Woodward (1871), the bulk of which came from Pichana with only a small proportion from Pebas. On the other hand, Boettger's fauna also includes all six species described by Gabb (1869) from Pebas itself. It is typical of the 'classic' Pebasian, though in common with the Pichana fauna, it lacks the several species of Thiaridae found at Iquitos, Canamá and Três Unidos.

Boettger's paper is reasonably well illustrated. The text, both on the palaeontology and the geological introduction, is of a high standard and it is clear, from the names used by him as well as from his comments, that he had a thorough grasp of previous work on the fauna, though he obviously was not aware of Conrad's two latest papers (1874*a*, *b*).

Pebas collections of Bassler (1925) *and Singewald* (1925)

Marshall (1928*a*) described some fossil naiades from the Pebasian of Pebas and of Paucarpata. Of the three from Pebas itself, two were collected by Singewald and the third by Bassler. Singewald's collection from the Upper Amazon was made in 1925 and sent to the United States Geological Survey in Washington. It came from a number of outcrops on Rio Marañón and Rio Napo (Gardner 1927: 507). Although Gardner's paper suggested that Singewald's collection was rich, the only fossils which appear to have been worked on are these naiades.

Unionacea from Pebas, described by Marshall, 1928*a*:

original determinations	revised determinations
PRODIPLODON BASSLERI Marshall (Bassler colln)	*Diplodon bassleri* (Marshall)
EODIPLODON GARDNERAE Marshall (Singewald colln)	*Diplodon gardnerae* (Marshall)
EODIPLODON PEBASENSIS Marshall (Singewald colln)	*Diplodon gardnerae* (Marshall)

Bassler's collection, made in the same year, 1925, is the only other mentioned in the literature as coming from Pebas. Willard's work (1966) may be regarded as an illustrated catalogue of Bassler's extensive collections from many different localities and horizons in Peru, and it deals with many different phyla. From his illustrations of Pebasian fossils it appears that not all of the determinations are accurate. Furthermore there are discrepancies between the plate descriptions and the various faunal lists. Willard's (1966) pl. 58, fig. 2, is correctly determined as *Pachydon erecta* Conrad from Pebas, but his pl. 58, fig. 3, also said to be of this species, is misidentified and is of a species I cannot name. It is a right valve, resembling that of *P. obliquus* Gabb, but the umbo is not far enough forward. This collection is now in Lehigh University, Bethlehem, Pennsylvania.

Bassler collection from Pebas, listed by Willard, 1966: 68:

original determinations	revised determinations
Corbula sp.	*Pachydon* sp.
Anisothyris obliqua (Gabb)	*Pachydon obliquus* Gabb
Anisothyris tenuis (Gabb)	*Pachydon tenuis* Gabb
Anisothyris erecta (Conrad)	*Pachydon erectus* Conrad
Anisothyris cuneata (Conrad)	*Pachydon cuneatus* Conrad
undetermined pelecypods	
Neritina puncta Etheridge	*Neritina ortoni* Conrad
Turbonilla minuscula Gabb	*Liris minuscula* (Gabb)
Turbonilla sp.	*Liris* sp.
Isaea ortoni Gabb	*Dyris ortoni* (Gabb)
'Anodontia'	indet. naiad
unidentified gastropods	

This list is in keeping with the small fauna originally described from Pebas by Gabb (1869). It contains four of the six original species. The undetermined gastropods and bivalves, together with two of Conrad's species of *Pachydon*, suggest that the Pebas fauna is reasonably rich and is perhaps comparable to the mainly Pichana fauna described in both Conrad's and Woodward's 1871 papers.

Pichana–Pichua–Cochaquinas–Pebas–Old Pebas

*(Conrad 1871*b*, 1874*a*, Woodward 1871)*

As mentioned previously, fossils collected from more than one locality by both Hauxwell and Steere were mixed. Conrad was sent, *via* Professor J. Orton of Vassar College, a collection made by Juan Hauxwell. Conrad (1871*b*: 192), when describing these fossils, quoted Orton as remarking 'a very few of these shells were found where I first discovered the deposit, which was at Pebas, near the mouth of the Ambiyacú; but the rest comprising nearly the whole collection, were obtained nearly 30 miles [50 km] below Pebas, on the South side of the Marañón, at Pichua, just West of Cochaquinas . . . and the shells appear to be more abundant even than at Pebas . . .' Conrad went on to comment (1871*b*: 192–193) on the excellent preservation of the fossils, and that specimens of both *Neritina* and *Pachydon* often retained the epidermis. He concluded that the fauna was not transported far and that it lived in either fresh or brackish water and was certainly not of marine origin.

Fauna of Conrad (1871*b*), mainly from Pichana:

original determinations	revised determinations
Isaea ortoni Gabb v, NYSM 9253	*Dyris ortoni* (Gabb)
Isaea LINTEA Conrad	*Dyris lintea* (Conrad)
LIRIS LAQUEATA Conrad v, NYSM 9259	*Liris minuscula* (Gabb)

original determinations	revised determinations
EBORA CRASSILIBRA Conrad	*Eubora crassilabra* (Conrad) *Eubora woodwardi* Kadolsky
EBORA (NESIS) bella Conrad	*Eubora bella* (Conrad)
Hemisinus SULCATUS Conrad v, NYSM 9226	*Hemisinus brasiliensis* (Moricand)
DYRIS GRACILIS Conrad v, NYSM 9192	*Dyris gracilis* Conrad
Neritina ORTONI Conrad (= *N. pupa* Gabb, *non* Linné)	*Neritina ortoni* Conrad
Bulimus LINTEUS Conrad	*Orthalicus linteus* Conrad
Pachydon tenuis Gabb	*Pachydon tenuis* Gabb
Pachydon CARINATA Conrad	*Pachydon carinatus* Conrad
Pachydon obliquus Gabb	*Pachydon obliquus* Gabb
Pachydon ERECTUM Conrad v, NYSM 8964	*Pachydon erectus* Conrad
Pachydon CUNEATUS Conrad v, NYSM 8963	*Pachydon cuneatus* Conrad
Pachydon OVATUS Conrad v, NYSM 9866	*Pachydon tenuis* Gabb
Pachydon ALTUS Conrad v, NYSM 8961	*Pachydon erectus* Conrad

The figured specimens, at least, are now in New York State Museum (NYSM), see Clarke (1906). Fifteen species are now recognized in the revised list of determinations. NYSM registration numbers are given for those species examined by me.

Woodward (1871) also published on what was probably another part of the same collection made by Hauxwell. This portion was sent in the first instance to a Mr Janson of Museum Street, London (Woodward 1871: 64). Woodward also acknowledged (1871: 64) the publication dated 10 October 1870 by Conrad *in advance of* the American Journal of Conchology. In this, Conrad's names were presumably no more than *nomina nuda*, at best in an abstract or advance programme, which I have not seen, for the scientific meeting at which the shells were to be exhibited. Woodward, however, in the systematic part of his paper gave Conrad's subsequent (1871*b*) plate and figure references. He must therefore have been in contact with Conrad in some way, or had the opportunity of studying either his paper or its prepublication proofs. It was not the report of the meeting (Conrad 1871*a*), which does not list the names.

Woodward's collection is in BMPD. It was not registered until 1922, some specimens in an unknown hand, but the bulk by the late Dr L. R. Cox. The register numbers are L27703–52 (LRC); G25284–99 (LRC); and G25472–87 (unknown hand). The usual entry in the register reads 'Cochaquinas, south side of the Marañón, valley of the Amazons', but the entry on G25472–87 reads 'some purchased from Hauxwell, some through Damon'. Original (or, at least pre-1922) labels with the specimens are rare. Apart from referring to Woodward's illustrations they give no more specific information than 'Tertiary, valley of the Amazons', whilst the rock sample LL27843 is labelled 'shell conglomerate, Tertiary, Valley of the Amazons, 2200 miles above Para, collected by Mr Hauxwell'.

This BMPD collection that Woodward studied contained well over 1000 shells, mainly *Pachydon* but with *Neritina* also common. The rock sample (LL27843) consisted of about 1 kg of rusty brown, indurated mudstone crowded with shells. Some 200 g of this block, and a further 100 g of matrix obtained from the apertures of *Neritina* and the interior of bivalves with both valves together, has been broken down using dilute hydrogen peroxide. Many small shells, representing both small species and also juveniles of large species, have been obtained.

Fauna of Woodward, main collection (listed 1871: 102–107):

original determinations	revised determinations
Ebora crassilabra Conrad **F**	*Eubora woodwardi* Kadolsky (*E. crassilabra* also present)
Ebora (Nesis) bella Conrad **F** (note)	*Eubora bella* (Conrad)
Neritina ortoni Conrad **F**	*Neritina ortoni* Conrad
Odostomia? sp. **F**	*Dyris ortoni* (Gabb)
Anodon BATESI Woodward **F**	*Anodontites batesi* (Woodward)
Anisothyris HAUXWELLI nom. nov. (for *P. tenuis* Gabb) **F**	*Pachydon tenuis* Gabb
A. hauxwelli var. α *distorta*	
A. hauxwelli var. β *crassa*	
Anisothyris (Pachydon) ovata (Conrad)	*Pachydon tenuis* Gabb
Anisothyris carinata (Conrad) **F**	*Pachydon carinatus* Conrad
Anisothyris (Pachydon) obliqua (Gabb) **F**	*Pachydon obliquus* Gabb
Anisothyris erecta (Conrad) **F**	*Pachydon erectus* Conrad
Anisothyris cuneata (Conrad) **F**	*Pachydon cuneatus* Conrad

Note. Although figured and present in the collection, *E. (N.) bella* was stated by Woodward to be absent: possibly it is from Damon's contribution, see below.

In the above list, figured species are marked '**F**'. The revised list of determinations contains eleven species, only one of which, *Anodonites batesi* Woodward, was not present in Conrad's (1871*b*) fauna.

After completing his paper, Woodward received a further collection, from the dealer Robert Damon of Weymouth, Dorset, which had been forwarded to him by Professor Orton. He added a post-script (1871: 108), which mentioned no new forms except:

original determinations	revised determinations
Isaea (Mesalia) ortoni Gabb	*Dyris ortoni* (Gabb)
Isaea tricarinata Conrad (*sic*)	*Dyris tricarinata* (Boettger, 1878)

Woodward commented that two different species had probably been placed together in *I. ortoni*: this is discussed in the systematic section, p. 192. *I. tricarinata* Conrad is a *nomen nudum* (p. 190).

Additional species. During the present study, the following species were found either un-named in the Hauxwell Collection, or extracted from washings of matrix. The first, *Dyris gracilis* Conrad, was present in Conrad's part of the Hauxwell collection. None of the other eleven species were found by either author. All the species attributed to Conrad in the list below were described by him later (1874*a*).

Dyris gracilis Conrad
Dyris HAUXWELLI sp. nov.
Liris ACICULARIS sp. nov.
Toxosoma eborea Conrad
Tropidobora tertiana (Conrad)
Vitrinella (*Vitrinellops*) *HAUXWELLI* sp. nov.
Vitrinella (*Vitrinellops*) sp.
?*Hebetancylus* sp. (? juv.)
Pachydon erectus elongatus (Boettger)
PEBASIA dispar (Conrad)
Ostomya papyria Conrad
Mytilopsis scripta (Conrad)
Mytilopsis sallei (Recluz)

The lists above of revised determinations, when combined, show a total of 28 species present in the Hauxwell collection.

This rich fauna, presumably mainly from Pichana, is most similar to that described by Boettger (1878) and also collected, by Hauxwell, from either Pichana or Pebas (or from both). Differences are minimal. Boettger's fauna lacks *Hemisinus brasiliensis* (Moricand), known from a single specimen. The other seven absentees are all from those easily overlooked, and mostly rare, additional species obtained recently from washings: *Dyris hauxwelli, Liris acicularis, Vitrinella* (*Vitrinellops*) *hauxwelli, V.* (*V.*) sp., *Pebasia dispar, Ostomya papyria* and *?Hebetancylus* sp.

These Hauxwell collection faunas also closely resemble the rich Iquitos fauna (de Greve 1938). Species not known from Iquitos are *Liris acicularis, Vitrinella* (*Vitrinellops*) *hauxwelli, V.* (*V.*) sp., *Hemisinus brasiliensis*, *Dyris gracilis*, ?*Hebetancylus* sp., *Ostomya papyria* and *Anodontites batesi*. Species not found in the Conrad/Woodward collections but occurring at Iquitos: *Liris scalarioides* (Etheridge), *Dyris tuberculata* (de Greve), *Vitrinella* (*Vitrinellops*) *degrevei* sp. nov., *Hemisinus kochi* (Bernardi), *Sheppardiconcha tuberculifera* (Conrad), *Sheppardiconcha coronata* (Etheridge), *Longiverena eucosmia* (Pilsbry & Olsson) and *Pachydon iquitensis* (de Greve). This last species is known only by one valve. Both *H. kochi* and *L. eucosmia* are rare, but the remaining species were described by de Greve as being either common or very common at Iquitos. Several of these are gastropods of the fresh-water family Thiaridae, and it may be that the Iquitos deposit represents a slightly less brackish facies. Comparison of the Unionidae is difficult, but the works of de Greve (1938) and Marshall (1928) suggest that the rare specimens of *Diplodon* from Iquitos and Pebas are similar.

Sheppard & Bate (1980) described the ostracod fauna listed below from the residue of matrix of the Hauxwell collection in BMPD.

(3) *Darwinula* sp.
(4) *Cypria AQUALICA* Sheppard & Bate
(5) *Perissocytheridea FORMOSA* Sheppard & Bate
(6) *RHADINOCYTHERURA AMAZONENSIS* Sheppard & Bate
(7) *Ambocythere CAMPANA* Sheppard & Bate
(8) *Cyprideis PURPERI PURPERI* Sheppard & Bate
(9) *Perissocytheridea*? *ELONGATA* Sheppard & Bate
(10) *BOTULOCYPRIDEIS SIMPLEX* Sheppard & Bate
(11) *OTAROCYPRIDEIS ELEGANS* Sheppard & Bate
(12) *Paracypris* sp.
(13) *Pontocypris* sp.

Species (1) and (2) are omitted because they only occur at La Tagua (p. 173). Species (3) and (7) also occur at La Tagua and a different subspecies of (8) also occurs there. Sheppard & Bate considered (4) to be indicative of fresh water, (5) and (8) to (11) of brackish water, whilst (6), (7), (12) and (13) suggested marine conditions. Their palaeogeographic conclusions are discussed later (p. 350).

The next collection from the Pebas/Pichana region was described by Conrad (1874*a*). It was made by Mr J. B. Steere, a graduate of Michigan University, who met Hartt whilst making natural history collections on the lower reaches of the Amazon. Hartt encouraged him to visit Pebas and record the geological section there and to collect fossils. Some details of Steere's findings were given in Conrad (1874*a*: 26) and Boettger (1878: 47–48). The most comprehensive account was reproduced in Hartt (1872: 55–56). Steere first saw fossils in clay beds just above Loreto, but did not have time to examine the exposure properly. Much of the river banks between there and Pebas were low and less than 100 ft (30 m) above river level during the dry season. The fossiliferous clay beds were low in the banks and overlain by 20–30 ft (6–9 m) of red clay comparable to the superficial clays so common on the Lower Amazon. Both Pebas and Pichana are situated on *tierra firme* (land not covered during the annual flood), some hundred feet (30 m) above the river level during the dry season.

Sections measured by Steere at Pebas (Hartt 1872: 56):

(a) In ravine near the road leading up the bank (to Pebas).

V	10 ft (3 m)	Surface deposit: red and white clay and sand, without fossils.
IV	5 ft (1.5 m)	Blue clay, full of fossils.
III	13 ft (3.9 m)	Blue clay; rare fossils, too poorly preserved to be extracted.
II	6 in (15 cm)	Seam of lignite; vegetable remains extend for few inches into clay both above and below seam.
I	15 ft (4.5 m)	Blue clay, with, in the centre, 3 ft (90 cm) band containing shells; base not seen.

Total, 43 ft 6 in. (*c.* 13 m)

(b) Not far from first section.

V	5–6 ft (1.5–1.8 m)	Red and white clay
IV	5 ft (1.5 m)	Dirty coal
III	3 ft (90 cm)	Blue clay filled with fossils
II	10 ft (3.0 m)	Blue clay
I	2–3 ft (60–90 cm)	Clay full of fossils

Total, 25–27 ft (5.5–6.1 m)

Steere also measured a third, but unfossiliferous, section nearby: this also draws attention to the fact that the thickness of the different bands varies markedly over short distances. Steere reported a similar succession at Pichana, whilst that at Old Pebas, which is at the mouth of Rio Ambiyacú, is denuded (? eroded or reduced). Steere also stated that bivalves were more numerous in the lower fossiliferous bands and gastropods in the upper (Hartt 1872: 57).

Unfortunately, Steere's fossils also became mixed, as becomes apparent from a letter from Steere to Hilgard, quoted by Conrad (1874*a*: 26). They came from three localities:

(1) Pebas 'one mile from the mouth of the Ambayacú'.
(2) Old Pebas 'two miles below'.
(3) Pichana 'perhaps fifteen miles from the mouth of the Ambayacú'.

Steere sent 'some shells that I know are new and bits of turtle shell, fish-bone, coral, crustaceans etc., which have not been noticed in the bed before.' Conrad, however, stated (1874*a*: 27) that he had found no coral in this or in any other collection of the Amazon fossils.

Steere collection of mixed fossils from Pebas, Old Pebas and Pichana, described by Conrad, 1874*a*:

original determinations (Conrad 1874*a*)	**revised determinations**
Pachydon (Anisorhynchus?) DISPAR Conrad v ANSP 31384	*PEBASIA dispar* (Conrad)
Pachydon altus Conrad, 1871 (lost)	*Pachydon erectus* Conrad, 1871 (see comment below)
Pachydon cuneata Conrad, 1871 (lost)	*Pachydon cuneatus* Conrad
Pachydon (Anisorhynchus) CUNEIFORMIS Conrad (lost)	indet. *Pachydon* sp.

original determinations	**revised determinations**
Dreissena (Mytiloides) SCRIPTA Conrad (lost) (note)	*Mytilopsis scripta* Conrad
Anodonta PEBASANA Conrad (lost)	*Anodontites* cf. *batesi* (Woodward)
Triquetra LONGULA Conrad (lost)	*Diplodon longulus* (Conrad)
OSTOMYA PAPYRIA Conrad (lost)	*Ostomya papyria* Conrad
Nuculana? sp. (lost)	indet. bivalve, possibly *Pachydon*
Planorbis sp. (lost)	probably *Vitrinella* (*Vitrinellops*) sp.
PACHYTOMA TERTIANA Conrad v ANSP 161151	*Tropidobora tertiana* (Conrad)
TOXOSOMA EBOREA Conrad ANSP 161152	*Toxosoma eborea* Conrad
CIRROBASIS VENUSTA Conrad (lost)	probably *Liris* sp.
LIOSOMA CURTA Conrad (lost)	*Toxosoma eborea* Conrad, juv.
CYCLOCHEILA PEBASANA Conrad (lost)	unknown
Hemisinus STEEREI Conrad (lost)	*Hemisinus* sp. indet. (worn)
Ebora crassilabra Conrad, 1871	*Eubora crassilabra* (Conrad)

Note. In the last line of his next paper, Conrad (1874*b*: 83) corrected *Mylitoides* (sic) to *Mytilopsis*. He was clearly referring to *Dreissena (Mytilopsis) scripta*.

Most of Conrad's type specimens are not listed as being present in ANSP in Richard's (1968) type catalogue. The registration numbers of those still known to exist are given above. Conrad's illustrations are poor, and there are also a number of inconsistancies in his text – such as mistaking left for right valves of bivalves. Conrad apparently suffered from poor health, and this may well be to blame.

Conrad (1874*a*: 32) also noted *Myliobates*, determined by Professor Leidy, and an impression in the clay of 'nearly a whole crab'. He mentioned the presence of *P. altus* and illustrated the species (1874*a*: 28; pl. 1, figs 4, 18). Immediately preceding the remarks on this species, he stated that there are no specimens in the collection which would represent *P. erectus*. However, the two are synonymous, and Conrad's figures truly represent this species.

This is an apparently unusual fauna from which several new genera were described by Conrad. In spite of so much of the type material being missing, it has been possible to suggest probable synonyms for several of the new taxa. The revised faunal list is of a typical Pebasian nature and is clearly similar to those described above for the Hauxwell mixed collection.

Canamá

(Brown 1879, Etheridge 1879)

There has been some controversy about the position of this locality, variously referred to as being either Brazilian or Peruvian. On modern maps and in the U.S. Government Gazetteer for Brazil, the only Canamá is marked as being on Rio Curuca, about 125 km upstream of its junction with Rio Javari, at 5° 37′ S, 72° 06′ W. However, Brown (1879: 79) stated that his fossils came from some 200 yards above the settlement of Canamá, which consisted of one or two houses in a clearing on a high bank of the Peruvian (northern) bank of Rio Javari. It lay some 50 miles (80 km) from the mouth of this river, where it joins Rio Marañón opposite Tabatinga. The account in Brown & Lidstone (1878: 483–485 and text illustration) is consistent with this. Canamá was described as the end of their journey up Rio Javari from Tabatinga. It is marked as such on their accompanying map which shows the extent of their travels. It is therefore confidently accepted that Brown's locality is where he described it. It is reasonably close to two other important localities, Três Unidos and Puerto Nariño.

Brown (1879: 78–79) also recorded the presence of similar fossils, without naming them, in 12 feet (*c.* 4 m) of grey clay at a place called Rebeiros (not in Gazetteer) some 20 miles (32 km) below the mouth of Rio Javari on the south bank of Rio Solimões. About 2 m above the fossiliferous Tertiary clay lay some 4 m of red and mottled grey and red clays which Brown considered to be a river deposit. He stated that the red clay contained a great abundance of small univalves. He also stated that fossils like those from Canamá, but usually with a preponderance of bivalves, occurred in grey clays exposed at several places along the banks of Rio Javari below Canamá. As well as molluscan fossils, he noted a band of lignite 2′ 6″ (75 cm) thick at a place called Barreiras Braga (not in Gazetteer). He also found *Unio* and *Anodon* and a gastropod unlike those occurring in the other sections. This suggests the possible presence of a third fossiliferous deposit, matching neither the grey clay of Canamá nor the red clay of the 'river deposit' at Rebeiros.

Section at Canamá (Brown 1879: 79):

River deposit (8′6″; 2.55 m):	
3′ (90 cm)	Reddish loam.
5′6″ (1.65 m)	Grey clay, mottled with iron-oxide stains.
Tertiary (37′8″; 11.40 m):	
1′ (30 cm)	Dull purplish clay, containing numerous casts of bivalves, chiefly *Anisothyris*.
14′ (4.25 m)	Slightly arenaceous bluish clays, containing great quantities of shells arranged in horizontal lines, chiefly of *Anisothyris* and *Neritina*.
1′ (30 cm)	Nodular concretionary clay-rock, the concretionary centres of which were composed of blue limestone, containing shells of same species as those in the clay.
14′ (4.25 m)	Greenish-blue slightly arenaceous clay, containing shells sparingly scattered through it, of similar genera to those in the beds above, and two thin layers of concretionary calcareous nodules.
1′8″ (50 cm)	Lignite.
6′ (1.80 m)	Light blue clay.

Brown records another section of 30′ 10″ (9.25 m) at the landing stage at Canamá. The top 10′ (3 m) was a yellowish clay and yielded *Melania, Cerithium* and *Anisothyris* as well as 'a very curious little species of *Neritina* marked with black dots' (surely *Neritina puncta* Etheridge, here placed in *N. ortoni* Conrad).

Brown went on to compare his sections with those measured by Steere (*in* Hartt, 1872) at Pebas. However, such detailed comparison of non-marine deposits, including thin bands of lignite, is not really possible. Brown, who was obviously well aware that his fauna was not typical of fresh water, thought that the sea must have reached far inland to perhaps 1,500 miles (2,400 km) west of the present shoreline during the deposition of the Canamá and Pebas deposits.

Like other early workers, Brown's collecting was obviously limited by lack of time and by constraints on carrying capacity. It is also a great pity that much of his collection was lost (see below). The details that he provided of his sections are of real value, as his writings (1879, Brown & Lidstone

1878) give the impression that he was a careful observer. He recorded *Neritina* and *Pachydon* (as *Anisothyris*) occurring together in great profusion. His second record is not so easy to interpret. These two genera were occurring in the same band as *Melania*, which (*sensu* Etheridge) is probably *Dyris* and *Liris*, as well as *Cerithium*, herein interpreted as *Sheppardiconcha coronata* (Etheridge). The genus is extinct but allied to *Hemisinus* and therefore thought to be exclusively fresh-water.

The fauna which Brown collected was described by R. Etheridge, sen. in an appendix to Brown's account (1879) of the geology. Etheridge's paper cannot be compared favourably with the earlier work of Woodward (1871) on the Pichana fauna. Etheridge listed an unjustifiably large number of genera – several of which have never been recorded since from the Pebasian – and named as new several species which were quite clearly the same as those described by previous authors. This was in spite of Hauxwell's collection (Woodward, 1871) being almost certainly available for comparison at that time in the British Museum.

Regrettably, much of Brown's collection was lost a long time ago and was never registered as part of the BMPD collections. Only 29 shells were registered, under 11 numbers, each representing one species, in the old B.M. Geology Department registers. The new gastropod and bivalve registers were not used until 1881: their issue presumably coincided with the reorganization at the time of moving the natural history collections from Bloomsbury to South Kensington. In the following faunal list, the Old Register numbers, together with the number of surviving specimens of each species, are indicated. The only other specimens known to be in existence are those, listed later, which were extracted from matrix in 1982.

The Canamá Fauna:

original determinations	**revised determinations**
Cerithium CORONATUM Etheridge. 97222 (×2)	*Sheppardiconcha coronata* (Etheridge)
Melanopsis BROWNI Etheridge (lost)	*Verena browni* (Etheridge)
Melania TRICARINATA Etheridge, *non* Boettger 1878. 97228 (×1)	*Dyris gracilis* Conrad
Melania BICARINATA Etheridge. 97726 (×3)	*Dyris gracilis* Conrad
Melania SCALARIOIDES Etheridge. 97724 (×2)	*Liris scalarioides* (Etheridge)
Pseudolacuna macroptera Boettger. 97723 (×3)	*Toxosoma eborea* Conrad
Natica? sp. (lost)	possibly *Eubora* sp.
Neritina PUNCTA Etheridge. 97222 (×2)	*Neritina ortoni* Conrad
Neritina ZICZAC Etheridge. 97232 (×3)	*Neritina ortoni* Conrad
Odostomia sp. (lost)	possibly *Dyris* sp.
Hydrobia DUBIA Etheridge. *Assiminea CRASSA* Etheridge. 97225 (×3)	?*Littoridina* (s.l.) *crassa* (Etheridge)
Isaea? ortoni? Conrad (lost)	*Dyris* sp. ?*ortoni* (Conrad)
Dyris? gracilis? Conrad (lost)	*Dyris* sp.
Fenella sp. (lost)	Could be either *Dyris* or *Liris* (see Wenz, 1940: 751, figs 2172–3).
Dreissena ACUTA Etheridge. 97230 (×3)	*Mytilopsis scripta* (Conrad) *Mytilopsis sallei* (Recluz). See below.
Anisothyris carinata (Conrad) (lost)	*Pachydon carinatus* Conrad
Anisothyris tenuis (Gabb) (lost)	*Pachydon tenuis* Gabb
Anisothyris hauxwelli Woodward (lost)	*Pachydon tenuis* Gabb
Anisothyris (Pachydon) TUMIDA Etheridge. 97229 (4 valves)	*Pachydon cuneatus* Conrad
Corbula CANAMAENSIS Etheridge. 97231 (4 valves)	*Pachydon erectus* Conrad
Thracia? sp. (small) (lost)	?*Ostomya* sp.
Lutraria? sp. (small) (lost)	?*Ostomya* sp. (? other valve)

Etheridge (*in* Brown 1879: 84) also discussed the specimens of *Anodon* and *Unio* referred to by Brown (1879: 80) from the cliffs a few miles below Canamá. Both specimens are lost; neither was ever registered.

Additional fauna. Some 50 g of clay became available whilst developing the specimens of *Mytilopsis* in 1982. The following additional species were extracted from this matrix.

Mytilopsis sallei (Recluz) – previously not visible, found under and obscured by *M. acuta*.
Pachydon obliquus Gabb
Pachydon TRIGONALIS sp. nov.
PEBASIA dispar (Conrad) – fragments only
fragments of indeterminate bivalve like *Ostomya*
Dyris lintea (Conrad), juv.
Dyris HAUXWELLI sp. nov.

Several valves of two ostracod species were also obtained, identified by R. H. Bate.

Cyprideis purperi Sheppard & Bate, 1980
Otarocyprideis elegans Sheppard & Bate, 1980

These specimens were not isolated until after the publication of the paper in which these species were described from elsewhere. Both species are indicative of brackish water and were described from the Hauxwell collection which came from the Pebasian, probably of Pichana. Interpretation of the synonymies given in Sheppard & Bate (1980) suggests that they also occur round San Paulo da Olivença (Purper 1977).

The revised determinations show the Canamá fauna to be typical of the Pebasian. It has not been possible to substantiate Etheridge's records of any of the genera which are either atypical or marine. I am unable to suggest any alternative determinations for Etheridge's small *Thracia* and *Lutraria* other than *Ostomya*. All three genera have similar shapes, with rounded anterior and posterior ends and with straight and almost parallel hinge lines and ventral margins. The shell of *Ostomya* is sometimes slightly corrugated. The different arrangement of the myophores in the two valves may have lead Etheridge to think that he was dealing with two different genera. The description he gives of his small ?*Natica*, with a slightly wavy outer lip, could well be of *Eubora*, a genus confined to the Pebasian.

Species of particular correlative value include *Sheppardiconcha coronata* (Etheridge) and *Verena browni* (Etheridge), both of which occur at Três Unidos and Igarapé da Extrema. The former is also known from Iquitos, whilst the latter occurs abundantly at the new locality of Puerto Nariño. A further link with this locality is provided by *Pachydon trigonalis* sp. nov. which is as yet unknown from elsewhere. *Toxosoma eboreum* Conrad, *Neritina ortoni* Conrad and the very rare *Pebasia dispar* (Conrad) are confined to the Pebasian. The suite of several species of *Pachydon* is typical and now includes the type species, *P. obliquus* Gabb. Both

Mytilopsis scripta Conrad and *M. sallei* (Recluz) are now listed in this fauna: the latter is one of the few Pebasian fossils indistinguishable from a still living species. Etheridge's descriptions of *Hydrobia dubia* and *Assiminea crassa* were apparently both based on the same specimens (Kadolsky 1980). This species is tentatively referred to as ?*Littoridina crassa*, but it may belong to an undescribed genus. It is not described here as new, partly because of the paucity of material and partly because of the existing confusion between the living genera *Littoridina* and *Heleobia*. This cannot as yet be resolved, because the type species of the former, *L. guidachaudi* (Souleyet), is so poorly understood. ?*L. crassa* is the only member of the Canamá fauna which is not known from other Pebasian localities.

Brackish elements of the Canamá fauna include *Pachydon* and *Neritina*, recorded by Brown as occurring together in profusion, as well as the much rarer *Mytilopsis* and *Pebasia*. No unequivocally fresh-water bivalves have been recorded from Canamá itself: both the *Unio* (Unionacea) and *Anodon* (Mutelacea) mentioned above came from several miles away. Two gastropods, the living *Verena* and extinct *Sheppardiconcha* (which is thought to be allied to *Hemisinus*) indicate a fresh-water environment. All the remaining gastropods belong to the Hydrobiidae, a family in which both genera and individual species may exhibit a wide salinity tolerance. No terrestrial gastropods are present.

The facies indicated by the Canamá molluscan fauna is fresh to weakly brackish and similar to conditions prevailing at Iquitos rather than in the possibly more strongly brackish Pichana deposit.

Três Unidos and Rio Quixito

(Oliveira & Carvalho 1924, Roxo 1924)

Oliveira & Carvalho (1924: 65–66) described a section and listed fossil molluscs, provisionally identified by J. C. Branner, which they had collected from Três Unidos in 1919. They described this as being a small settlement on the Peruvian (left or north) bank of Rio Javari, inhabited by three Brazilians. It is marked as Profile (perfil) no. 6 on their map. The course of Rio Javari as shown on their map coincides well enough with that seen on modern maps. Their locality thus approximately corresponds with 40° 24′ S, 71° 13′ W, although other sources have suggested that it lies elsewhere (see below). Further confirmation that the position of Três Unidos is as stated here is provided by del'Arco *et al.* (1977: 51 and geological map), who referred to this classic locality as being near their own Locality 4 of Jarina, from where they had collected un-named molluscs in 1975. The correct positioning of Três Unidos now shows that it is about 120 km south-west of the new locality of Puerto Nariño, Colombia and about 80 km south-west by west of Canamá (Brown 1879, Etheridge 1879), which also lies on the Peruvian bank of Rio Javari.

Oliveira & Carvalho during their expedition of 1919 also collected small faunas from Cachoera (rapids or waterfall) de Tracoás (1924: 71, map – perfil no. 14) and Igarapé de Extrema de Manoel Honorato (perfil no. 15). Both of these localities, which are not marked very precisely on their map, lie on Rio Quixito, about 20 km apart in the region of 4° 35′ S, 70° 37′ W. See pp. 330–331.

Oliveira & Carvalho's faunas were dealt with in more detail by Roxo (1924), who figured several species and described two as new. Most of the gastropods have been the subject of competent and well-illustrated partial systematic revisions by Santos & Castro (1967) and by Costa (1981), whilst some were either figured or otherwise mentioned in Parodiz (1969). None of the bivalves have been revised. Roxo (1924) also discussed Pebasian species which were not present in the Três Unidos fauna, but their absence may not always have been appreciated by subsequent authors. Because of this and later changes in determinations, it is not possible to compile a definitive list of this fauna, working from the literature alone.

There have been conflicting views about the positions of these localities. The Três Unidos of Oliveira & Carvalho is not the same as the only entry under that name, of a presumably larger place, listed in U.S. Government Gazetteer for Brazil at 6° 37′ S, 69° 33′ W, nor is it as marked on de Greve's map (1938: pl. 10), much further up Rio Javari at 5° 40′ S, 73° 20′ W, lying almost due south of Iquitos. Roxo (1924) referred to 'Cachoera de Fracos' and 'Fracoas' instead of Tracoás. Del'Arco *et al.* (1977: 51) stated that it was difficult to position 'Cachoera das Fracoas' and Igarapé da Extrema exactly, as they were not shown on their map.

Del'Arco *et al.* also listed some 37 fossiliferous localities, many of which had yielded only un-named bone or plant fragments. Fossil molluscs occurred at several, but were not named except from two (Locs 13 and 28). Loc. 13 at Atalaia del Norte, supposedly Pliocene, has yielded *Aylacostoma* and *Pachydon*: Pebasian fossils have been described from this area (Purper 1977, ostracods; Costa 1980, molluscs). Loc. 28 at Aquidabã, on Rio Jurua (6° 30′ S; 69° 40′ W), supposedly Pleistocene, has yielded a fauna lacking typical Pebasian elements, but with strong resemblances to the living Amazonian fauna. It contains *Ampullaria, Aylacostoma, Hydrobia, ?Doryssa, Helix* and *Stenogyra*, several genera of Unionacea, *Anodontites* (Mutelacea) and *Pisidium* (Corbiculacea), as well as a rich vertebrate fauna. It is covered in greater detail in several works (Roxo 1937, Moura & Wanderley 1938, Oliveira 1940, Oliveira & Leonardos 1943: 636, map – fig. 156, and Palmer 1945). The previously held view that this fauna is of Pebasian age can no longer be supported.

The molluscan localities (2–9 and 13) listed as being Pliocene (i.e. Pebasian on their dating) by del'Arco *et al.* (1977: 51–52) all lay in the Atalaia del Norte–Benjamin Constant region and near the mouth of Rio Javari. None lay on Rio Quixito, so it appears that there has been no follow-up of Oliviera & Carvalho's collecting expedition of 1919. Del'Arco *et al.* (1977: 51) wrote that fossil molluscs of the Pliocene localities were comparable to those of Pebas and Iquitos and that confirmation of this dating was provided by the armadillo *Kraiglievichia*. In support, they quoted (1977: 53) the identification by Dr Bryan Patterson of *K. paranense* from their Loc. 18 on Rio Jutaí. This, however, is one of a series of vertebrate localities lying some 150 km to the south-east of Benjamin Constant and also in the area yielding their Pebasian molluscan faunas. Thus, the brackish-water Pebasian localities and the presumably terrestrial or near-terrestrial vertebrate localities lie rather far apart and represent rather different facies which may or may not be contemporaneous. No faunal elements common to both have so far been described, so there is, as yet, no palaeontological evidence as to their relative ages. Del'Arco *et al.* mapped both their molluscan and their vertebrate localities as Solimões Formation.

The following section of the bank of Rio Javari at Três Unidos was given by Oliveira & Carvalho (1924: 66):

—	Top soil
0.20 m	white clay
0.15 m	lignite
0.20 m	dark clay
1.70 m	dark clay, rich in Tertiary fossils, and with fragments of lignite disseminated throughout
5 m	bluish grey clay with greenish calcareous inclusions
———	river level ———

They listed (1924: 67) the following fauna, identified by J. C. Branner:

Dreissena fragilis Boettger
Anisothyris (Pachydon) tenuis (Gabb)
Anisothyris (Pachydon) carinata (Conrad)
Anisothyris erecta (Conrad) (See below)
Leila (Iridina) sp. nov.
Hydrobia ortoni (Gabb)
Hydrobia scalarioides (Etheridge)
Hydrobia lintea (Conrad)
Hydrobia tricarinata (Boettger)
Pseudolacuna macroptera (Boettger)
Melanopsis browni Etheridge
Cerithium coronatum Etheridge
Neritina zig-zag [no author; presumably *N. zic-zac* Etheridge rather than *zig-zag* Lamk.]

Roxo's fauna (1924) differs slightly. It is not known whether he studied the same specimens as Branner or whether the collection was split between them. The few species figured by Roxo are indicated. Revised names are given in the second column. The generic names are always those used throughout the present work. Species revised in Santos & Castro (1967) are indicated thus *; by Costa (1981) thus †; specific name changes instigated in the present paper, thus +. Roxo's material is in Departamento de Paleontologia do Museu Nacional do Rio de Janeiro (DP, MN).

original determinations		**revised determinations**
Anisothyris hauxwelli Woodward	+	*Pachydon tenuis* Conrad
Anisothyris carinatus (Conrad)		*Pachydon carinatus* Conrad
Anisothyris cuneatus (Conrad)		*Pachydon cuneatus* Conrad
Anisothyris obliqua (Gabb)		*Pachydon obliquus* Gabb
Anisothyris tumida Etheridge	+	*Pachydon cuneatus* Conrad
Tellina amazonensis Gabb		*Pachydon amazonensis* (Gabb)
Dreissena acuta Etheridge (fig. A)	+ +	*Mytilopsis sallei* (Recluz) *Mytilopsis scripta* (Conrad)
Anodonta fragments		?*Anodontites*
Hyria corrugata (Lamarck)		?*Triplodon corrugatus* (Lamarck)
Cerithium coronatum Etheridge	*†	*Sheppardiconcha coronata* (Etheridge)
Melanopsis? browni Etheridge	†	*Verena browni* (Etheridge)
Melania tricarinata Etheridge		*Dyris* sp.
Melania bicarinata Etheridge		*Dyris* sp.
Melania scalarioides Etheridge (see below)	+†	*Liris scalarioides* (Etheridge)
Neritina ortoni Conrad (included *N. pupa* Gabb, *non* Linné)		*Neritina ortoni* Conrad
Neritina puncta Etheridge	+	*Neritina ortoni* Conrad
Neritina ETHERIDGI Roxo, nom. nov. pro *Neritina ziczac* Etheridge, *non* Lamarck	+	*Neritina ortoni* Conrad
(fig. B is un-named *Neritina*)		——
Pseudolacuna macroptera 'Etheridge' (*sic*)	†	*Toxosoma eboreum* Conrad
Ebora crassilabra Conrad		*Eubora* sp.
Hydrobia dubia Etheridge (see below)	+	?*Littoridina crassa* (Etheridge)
Odostomia sp. (of Woodward, 1871)		*Dyris* sp.
Isaea (Mesalia) ortoni Gabb	†	*Dyris ortoni* (Gabb)
Isaea lintea Conrad	†	*Dyris lintea* (Conrad)
Purpura WOODWARDI Roxo, nov. sp. (figs C, D)	+*	*Verena ?crenocarina* (Moricand)
Planorbis BOURGUYI Roxo, nov. sp. (fig. E)	+	?*Vitrinella* (s.l.)

Several questions about the Três Unidos fauna must remain unanswered at present and can only be resolved by re-examining the material. First, Branner (*in* Oliveira & Carvalho 1924) identified *Anisothyris* [i.e., *Pachydon*] *erecta* Conrad, but Roxo (1924: 44) stated that *Corbula canamaensis* Etheridge (which is a synonym) was absent. Secondly, there is the rather similar case of *Assiminea crassa* Etheridge which was stated by Roxo (1924: 48) to be absent whilst its synonym *Hydrobia dubia* Etheridge was thought to occur in abundance (1924: 48). *Liris* is recorded variously as *Melania scalarioides* (1924: 46, present at Três Unidos), *Turbonilla minuscula* (1924: 48, unlocalized) and as *Liris laqueata* (1924: 48, absent). The specimen figured by Costa (1981: pl, 1, figs 9, 10) as *L. minuscula* (Gabb) is large for the genus and is provisionally identified as *L. scalarioides* (Etheridge). It must therefore be assumed that these and similar apparent contradictions, such as with *Melania, Dyris, Hydrobia, Odostomia* and *Isaea*, were due to difficulties encountered by Roxo in interpreting the often inadequate descriptions and illustrations provided by earlier authors.

Roxo listed the following species as not occurring in his fauna. *Corbula canamaensis* Etheridge, *Fenella* sp. of Etheridge, *Nesis bella* Conrad, *Dyris gracilis* Conrad, *Liris laqueata* Conrad, *Hemisinus sulcatus* Conrad, *Bulimus linteus* Conrad and *Natica* spp. of both Conrad (1871*b*) and Etheridge (1879).

Purpura woodwardi Roxo was taken by several workers, including Roxo himself, to be evidence of marine conditions. However, it clearly belongs to the fresh-water genus *Verena*.

The status of *Planorbis bourguyi* Roxo is uncertain. Although it is figured (fig. E), there is no description. Roxo stated that two out of the three small shells in his collection had been lost and expressed the hope that a diagnosis could be provided if more specimens were discovered later among the great quantity of material available. It thus appears to be valid. From Roxo's figure, it seems likely to belong to *Vitrinella*, s.l.

Três Unidos has yielded a typical Pebasian fauna with *Pachydon, Eubora, Toxosoma, Dyris* and *Liris*. *Verena browni* Etheridge is known only from three other localities, none of which are far away, Puerto Nariño, Igarapé da Extrema and its type locality, Canamá.

Cachoera de Tracoás

Oliviera & Carvalho (1924: 71) gave no faunal list for this locality (perfil no. 14). The following list has been extracted from Roxo's text (1924): the names are revised to conform with those used in the present paper.

original determinations	**revised determinations**
Anisothyris hauxwelli Woodward	*Pachydon tenuis* Gabb
Anisothyris carinata (Conrad)	*Pachydon carinatus* Conrad
Anisothyris amazonensis Gabb	*Pachydon amazonensis* (Gabb)
Unio sp.	Unionacea/ Mutelacea
Melania tricarinata Etheridge	*Dyris* sp., ? *tricarinata* (Boettger)
Melania bicarinata Etheridge	*Dyris* sp.
Melania scalarioides Etheridge	*Liris scalarioides* (Etheridge)
Odostomia sp.	?*Dyris* sp.

This appears to be a typical, but not very rich, Pebasian fauna.

Igarapé da Extrema de Manoel Honorato

Oliviera & Carvalho (1924: 71) listed some fossils from this locality on Rio Quixito (perfil no. 15). A few fossils from here are also mentioned in Roxo's text (1924) and are indicated thus *.

original determinations	**revised determinations**
Anisothyris (Pachydon) carinata Conrad	*Pachydon carinatus* Conrad
Tellina amazonensis Gabb	*Pachydon amazonensis* (Gabb)
Dreissena acuta Etheridge	*Mytilopsis sallei* (Recluz) *Mytilopsis scripta* (Conrad)
Melania escalarioides Etheridge (*sic*)	*Liris scalarioides* (Etheridge)
Ebora crassilabra Conrad	* *Eubora sp.*
Pseudolacuna macroptera Boettger	* *Toxosoma eborea* Conrad
Cerithium coronatum Etheridge	* *Sheppardiconcha coronatum* (Etheridge)

In addition, Roxo (1924: 46) recorded *Verena browni* (Etheridge) from this locality (as ?*Melanopsis browni*). Thus, the fauna of Igarapé da Extrema is typical of the Pebasian and has particular resemblances to those of the neighbouring localities of Três Unidos, Canamá and Puerto Nariño.

Iquitos

(De Greve 1938)

A large collection of molluscs from Iquitos (3° 42′ S, 73° 42′ W) was made in 1912 by a Swiss expedition under Professor B. Peyer. This was monographed by de Greve (1938), who (1938: 15–18) briefly described the six localities in the vicinity of the town from which the fauna was obtained. The maximum section appears to be of some 6.80 m, mainly of blue clays, but including a 0.5 m lignite band (1938: 16). De Greve's is the most comprehensive and best illustrated work on the palaeontology of any of the Pebasian localities to date. It has probably been used for identifications by all subsequent workers not having easy access to type material. For instance, Wenz (1939) reproduced de Greve's figures to illustrate *Liris* and *Dyris*. Unfortunately, the figure of *Liris* was of a species probably belonging to *Dyris* rather than of its type species, whilst the illustration of *D. gracilis*, the type species of *Dyris*, was misidentified.

The deposits at Iquitos have been dealt with in a few other works. Steere (*in* Hartt, 1872: 56) reported the presence at Iquitos of beds similar to those at Pebas, but could find no fossils. Conrad (1874*b*) described two species, listed below, collected by Orton on a second visit to the region.

Iquitos fossils collected by Orton, described by Conrad (1874*b*).

original determinations	**revised determinations**
HAPLOTHAERUS CAPAX Conrad (lost)	*Anodontites* sp.
Hemisinus TUBERCULIFERUS Conrad	*Sheppardiconcha tuberculifera* (Conrad)

Haplothaerus capax was described from a broken specimen, not listed in Richards (1968). Conrad stated that *Hemisinus tuberculiferus* was very common. The type series is in ANSP: a specimen was figured by Pilsbry (1944), who did not indicate whether it was Conrad's figured syntype.

Ruegg & Rosenzweig (1949), in a paper reviewing current thinking on the Pebasian sediments, gave a map of the town area and also geological sections indicating that underneath a layer of alluvium, there was a thickness of some 35 m of grey, blue and black clays with lignite. The bottom of the clay was not reached. This sequence is much thicker than that indicated by de Greve.

Willard (1966: 65) listed a few fossils from Iquitos, collected by Bassler in 1922. He also figured two further species, not on his faunal list, as coming from Iquitos. Bassler visited several localities in the district which yielded similar small faunas, almost exclusively of the more common species. They add little to our knowledge of the fauna, but are a useful indication of the widespread nature of the Pebasian deposits around Iquitos.

Iquitos fossils collected by Bassler in 1922, recorded in Willard (1966).

original determinations	**revised determinations**
Anisothyris obliqua (Gabb)	*Pachydon obliquus* Gabb
Anisothyris erecta (Conrad)	*Pachydon erectus* Conrad
Anisothyris cf. *erecta* (Conrad)	——
Hydrobia tricarinata Boettger	*Dyris tricarinata* (Boettger)
Hydrobia confusa Boettger	*Dyris ortoni* (Gabb)
Anodontites lacivansis (*sic*) Pilsbry & Olsson (pl. 56, fig. 2)	unidentifiable naiad
Anisothyris cf. *tenuis* (Gabb) (pl. 58, fig. 1)	*Pachydon* cf. *tenuis* Gabb

Bassler's collection is now at Lehigh University, Bethlehem, Pennsylvania.

De Greve (1938) refigured several of Boettger's (1878) type specimens, which come from either Pebas or Pichana. In fact, in the case of some species, all his figured specimens are taken from Boettger's collection and none are of Iquitos shells. Furthermore, in his text, he gave the dimensions of Boettger's shells even though in his faunal list (1938: 125) he indicated that the particular species was very common at Iquitos (i.e. *Hydrobia ortoni, H. confusa* and *H. tricarinata*). On the other hand, there are species such as *Lacuna (Ebora) bella* (Conrad) which de Greve dealt with in his text (1938: 72–73) but neither figured nor placed on his faunal list. This omission of illustrations of Iquitos shells is unfortunate as study of several of these species from different localities seems to show some purely local variation. Kadolsky (1980) recognized three species of his genus *Eubora* in the sample of shells that de Greve had identified as belonging to a single species (see faunal list below). Further revisory work might well reveal similar examples in different genera. Care is therefore necessary in assessing the contents of de Greve's fauna. The species which he actually identified as occurring in Peyer's collection from Iquitos were listed by him (1938: 125) and, in addition, he indicated their registration numbers in the text after their description and measurements.

Iquitos fauna, collected by Peyer Expedition, described by de Greve (1938).

All the species listed below, with very few exceptions, were illustrated by de Greve. Key: Figured specimens from Iquitos only, *; from either Pebas or Pichana (*ex* Boettger, 1878), B; from both collections *B; not figured O. R, rare; C, common; VC, very common (after de Greve, p. 125). v, examined herein. The collection is in PIMUZ.

original determinations	revised determinations
Neritina ortoni Conrad *C	*Neritina ortoni* Conrad
Neritina AMAZONENSIS de Greve v*R	*Neritina ortoni* Conrad
Neritina ROXOI de Greve v*R	*Neritina ortoni* Conrad
Neritina etheridgei Roxo v*R	*Neritina ortoni* Conrad
Helicina (?) tertiana (Conrad) *R	*Tropidobora tertiana* (Conrad)
Lacuna (Ebora) crassilabris (Conrad) *C	*Eubora woodwardi* Kadolsky *Eubora grevei* Kadolsky *Eubora pygmaea* Kadolsky
Pseudolacuna macroptera Boettger *VC	*Toxosoma eborea* Conrad
Ampullaria sp., fragments C	——
Hydrobia (Conradia) ortoni (Gabb) vB, VC	*Dyris ortoni* (Gabb)
Hydrobia (Conradia) confusa Boettger B, VC	*Dyris ortoni* (Gabb)
Hydrobia (Conradia) tricarinata Boettger B, VC	*Dyris tricarinata* (Boettger)
Hydrobia (Conradia) lintea (Conrad) *VC	*Dyris lintea* (Conrad)
Dyris gracilis Conrad *C	*Dyris HAUXWELLI* sp. nov.
Liris laqueata Conrad *B, VC	*Liris minuscula* (Gabb)
Liris minuscula (Gabb) *VC	*Liris scalarioides* (Etheridge)
Liris TUBERCULATA de Greve v*VC	*Dyris tuberculata* (de Greve)
Semisinus sulcatus (Conrad) v*R	*Hemisinus kochi* (Bernardi)
Semisinus tuberculiferus (Conrad) v*C	*Sheppardiconcha tuberculifera* (Conrad)
Semisinus PEYERI de Greve v*R	*Longiverena eucosmia* (Pilsbry & Olsson)
Cerithium(?) coronatum Etheridge *C	*Sheppardiconcha coronata* (Etheridge)
Planorbis sp. v*R	*Vitrinella* (*Vitrinellops*) *DEGREVEI* sp. nov.
Anodontites sp. (p. 125, ?= 'Nayad shell' of p. 19, text-fig. 1) C	*Anodontites* sp.
Hyria sp. *R	*Diplodon ?longulus* (Conrad)
Anisorhynchus JEANNETI de Greve *R	*PEBASIA dispar* (Conrad)
Anisothyris amazonensis (Gabb) *B, R	*Pachydon amazonensis* (Gabb)
Anisothyris tenuis (Gabb) *VC	*Pachydon tenuis* Gabb
Anisothyris cuneata (Conrad) R	*Pachydon cuneatus* Conrad
Anisothyris ovata (Conrad) O, R	*Pachydon tenuis* Gabb
Anisothyris erecta (Conrad) B, VC	*Pachydon erectus* Conrad
Anisothyris erecta (Conrad) var. *elongata* Boettger B, C	*Pachydon erectus elongatus* (Boettger)
Anisothyris obliqua (Gabb) *VC	*Pachydon obliquus* Gabb
Anisothyris IQUITENSIS de Greve *R	*Pachydon iquitensis* (de Greve)
Anisothyris carinata (Conrad) *C	*Pachydon carinatus* Conrad
Congeria fragilis Boettger B (Boettger collection only, does not occur at Iquitos)	
Congeria cf. *fragilis* Boettger *R *Congeria* n. sp. aff. *fragilis* Boettger *C (and nov. vars I to IV) *Congeria* cf. *acuta* (Etheridge) O, R *Congeria scripta* (Conrad) *R	*Mytilopsis sallei* (Recluz) and *Mytilopsis scripta* (Conrad)

In addition, de Greve described, under 'Problematicum', a possible member of the Porifera, *IQUITOSIA BLUNTSCHLII* (1938: 110, text-figs 24, 25) and (as 'Vermes') a small adherent polychaete (1938: 108; pl. 3, figs 29, 30). This polychaete has also been extracted (1982) from the Hauxwell collection matrix, probably from Pichana.

The Iquitos molluscan fauna (Conrad 1874*b*), de Greve 1938) is one of the richest Pebasian fauna so far known. It comprises 31 named species. The only specifically unnamed taxa are the *Ampullaria* sp. and *Anodontites* sp. of de Greve and the unidentifiable naiad of Willard: both of the latter might be the same as *Haplothaerus capax* Conrad. The main absentee is *Verena browni* (Etheridge), described from Canamá, and very common at both Três Unidos and Puerto Nariño. Other species not present are rare, and with the exception of naiades such as *Anodontites batesi* (Woodward) are also small and therefore easily overlooked: these include *Ostomya*, the smaller species of *Vitrinella* (*Vitrinellops*) and *Dyris gracilis* Conrad.

Two living species are present. This is the only known fossil occurrence of *Hemisinus kochi* (Bernardi). The earliest known occurrence of *Mytilopsis sallei* (Recluz), however, is in the late Oligocene of Panama. Only a few taxa present also occur in non-Pebasian deposits. *Pachydon cuneatus* Conrad was recorded by Rutsch (1952) from the Neogene of Venezuela. A specimen of *Neritina*, very similar to *N. ortoni*, was recorded from the marine Miocene (now thought to be N.8) of the Paraguana Peninsula, Venezuela by Jung (1965) as *N.* aff. *woodwardi* Guppy, a very different species. Specimens identified as *Dyris tricarinata* (Boettger) are identified herein as occurring in the Neogene San Cayetano Formation of the Loja Basin, Ecuador (Bristow & Parodiz 1982), but this appears to be a very variable species upon which too much stratigraphical reliance should not be placed. *Mytilopsis scripta* (Conrad), according to the synonymy constructed herein, also occurs in the La Cira fossil horizon of the Middle Magdalena Valley (Pilsbry & Olsson 1935) and at La Tagua, Colombia as well as in probable late Oligocene strata of western Peru (Olsson 1931). A further link with strata of the Middle Magdalena Valley is provided by the reidentification of *Semisinus peyeri* de Greve as *Longiverena eucosmia* (Pilsbry & Olsson 1935). This species now has several synonyms and is believed to occur not only in the type horizon, the Mugrosa fossil band, but also in the La Cira fossil band, and is recorded from the Miocene of the Cuenca Basin as *H. peyeri dickersoni* by Palmer (*in* Liddle & Palmer 1941). *L. colombiana* sp. nov. from La Tagua is a very similar species.

The age of the Magdalena Basin faunas is still in dispute and is discussed further in the next section (p. 333), where it is concluded that the Mugrosa and La Cira horizons are not of very different ages and that the older of the two, the Mugrosa, is not likely to be older than latest Oligocene and might even be early Miocene. The combined occurrence in the Iquitos fauna of a few species from the Magdalena Basin faunas (one of which also occurs in the Miocene of the Cuenca Basin) with two living species suggests that the

Iquitos is no older than Miocene, and is likely to be later than Lower Miocene.

It is difficult to put an upper limit on the age of the Iquitos fauna. It is, like others from the Pebasian, very different from that of the present day Amazon Valley, except for the presence of the living *Hemisinus kochi* (Bernardi). The only other living species is *Mytilopsis sallei* (Recluz) from no nearer than the Caribbean. This rather marked lack of Recent elements, even at generic level, is evidence of a considerable change in conditions between the time of deposition of the Iquitos sediments and the present day. This, in itself, cannot be construed as proof that this deposit is particularly old. Considerable changes have occurred in many parts of the world during the Pleistocene. The differences apparent in the Amazon region, though striking, are of a comparable order of magnitude. The distribution, discussed above, of the comparatively few fossil species known from other faunas points to a Miocene rather than a later age. It is therefore concluded that the Iquitos fauna is more likely to be Middle to Upper Miocene in age than either earlier or later.

This Iquitos collection is both rich and with reliable locality data, and is thus the best example of the Pebasian fauna available for ecological assessment. De Greve (1938: 17, table 1) showed the distribution of genera at his six Iquitos localities. Genera here considered to be indicative of either brackish or fresh water occur with other genera typical of truly fresh water. There is no apparent indication that any particular locality is either more or less saline than any other. *Pachydon* occurs at all six, whilst *Mytilopsis* and *Liris* occur together at four localities (I, II, V and VI). The taxa with the widest salinity tolerance are *Neritina* and *Pachydon*, both of which are very common, along with the moderately common *Mytilopsis*. None of the Hydrobiidae (Littoridininae, Lithoglyphinae and Cochliopinae) can be regarded as definitely indicative of either brackish or fresh-water. All the Thiaridae (*Hemisinus, Longiverena*, and presumably also the related but extinct *Sheppardiconcha*) are fresh-water genera. *Hemisinus*, however, occurs both in South America and on Caribbean islands, so it must have exhibited tolerance to salt water at some stage in its life history unless all its occurrences on islands are human introductions. Some of these appear from de Greve's (1938: 125) assessment to be moderately common, but they are by no means a dominant part of the fauna.

As is the case with other Pebasian faunas, the exclusively fresh-water naiades (Unionacea and Mutelacea) are comparatively rare. Bivalves of the fresh-water Superfamily Corbiculacea are not known from Iquitos, nor are aqatic or terrestrial pulmonate gastropods. The amphibious (fresh-water and terrestrial) prosobranch *Ampularia* is known only from fragments, apparently obtained from a lignite band, and does not occur with the rest of the molluscan fauna.

The preservation of the shells figured by de Greve (1938) is excellent, except for the apertures of gastropods which are often broken. It is concluded that the clays of the Iquitos deposit were laid down in an area, such as a lagoon or series of lagoons, in which saline and fresh water could mingle. This probably bordered a low-lying, densely forested region which provided the material for the lignite bands.

Magdalena Valley, Colombia

The non-marine Tertiary outcrops over large areas of the Magdalena Valley, and from this region came the only previously-described molluscan faunas from Colombia of relevance to the present study. Anderson (1928) described as Eocene a small fauna from near San Juan de Rio Seco in the Upper Magdalena valley. He also published on the stratigraphy of the region (1927). Below, it is suggested that this fauna came from the Santa Teresa Formation and is probably Miocene in age.

Pilsbry & Olsson (1935) described three faunas from the Middle Magdalena Valley: the last section of their paper was contributed by Wheeler and was on the stratigraphy. Their conclusions were that the Los Corros faunas was Eocene, the Mugrosa was Middle Oligocene, and the youngest, the La Cira, was Upper Oligocene to Lower Miocene. Here it is suggested that there is no molluscan palaeontological evidence for the age of the Los Corros fauna more precise than 'probably Palaeogene'. It also appears that the Mugrosa, which has species in common with the La Cira, is not much older than the latter. The former is unlikely to be earlier than Late Oligocene and may be younger, while the latter is almost certainly Miocene. The La Cira is tentatively correlated both with Anderson's (1928) fauna and with the new La Tagua faunas.

Wheeler's (1935: 33–34) account of the stratigraphy of the Middle Magdalena Valley indicated that the La Cira fossil horizon consisted of several distinct fossiliferous bands in some 350 ft (105 m) of sediments lying at the top of the Colorado series, which varies in thickness between 2600 and 6900 ft (780–2070 m). Below this lay the Mugrosa Formation, which varied in thickness between 1200 and 4500 ft (360–1350 m). Its topmost bed, the Mugrosa fossil horizon, was between a few inches and 25 ft (up to 7.5 m) thick, and could be traced for some 75 miles (120 km). The Mugrosa was underlain immediately by the Los Corros fossil horizon, some 30–50 ft (9–15 m) thick, forming the topmost part of the Esmeraldas Formation of the Chorro Series.

Molluscan faunas similar to those discussed above have been reported, but never illustrated, by Butler (1939, 1942) and de Porta (1966, 1974), the last reference being to his *Lexique Stratigraphique* volume on the Tertiary of Colombia.

Palynological dating

At this point, it seems appropriate to discuss briefly the work on palynological dating, as applied to these Tertiary non-marine deposits of Colombia. In later works (Hopping 1967, Germeraad *et al.* 1968), it is apparent that palynologists have successfully matched their zones with those erected on planktonic foraminifera. In earlier works (van der Hammen 1957, 1961), neither spore nor foraminiferal zones were named. A difficulty with all these papers is that it has been virtually impossible to equate actual molluscan localities with the material, much of which came from boreholes, worked on by palynologists.

LA CIRA FORMATION. Van der Hammen (1957: 67) placed this in the Upper Oligocene. In discussing the age, he mentioned both the molluscan fauna from the Middle Magdalena Valley described by Pilsbry & Olsson (1935) and the vertebrates from near La Dorada, from much higher in the Magdalena Valley (Stirton 1953). Stirton's material comes from nowhere near the molluscan fauna localities. Although no indication of the localities yielding the spore flora was given, it is clear from his later work (van der Hammen 1961: 102) that his interpretation of the La Cira was the same as that of Wheeler (1935: 34): he considered it the top of the Colorado Series (or Formation). In the same work, however, (1961: 106) he wrote that the La Cira of the Upper Magdalena Valley corresponded to the Colorado Formation (i.e. as a whole, rather than the uppermost part). The Colorado was also dated as Upper Oligocene. Van der Hammen (1957: 90) had explained that his usage of the term Upper Oligocene followed that of Stainforth (1948) rather than of Eames (1953). Thus, his dating of the La Cira and Colorado Formations places them both within the Lower Miocene, in present-day terminology.

Hopping (1967: 38–42, figs 10, 11) discussed in great detail the distribution of the stratigraphically important *Crassoretrilites vanraadshooveni* (*nom. nud.*, validated Germeraad, Hopping & Müller 1968: 287; pl. 1, fig. 3). In the Magdalena Valley its first occurrence is in the lower part of the Real Formation, just above the top of the La Cira Formation which lay entirely within the Zone of *Verrutricolporites rotundiporis*. Hopping (1967: 46, fig. 13) showed the base of this zone coinciding more or less with the top of the zone of *Globigerina ciperoensis ciperoensis* (now Zone P22, whose top is about 22.5 m.y. old, and is just below the Oligo-Miocene boundary). The base of the *C. vanraadshooveni* Zone was shown in the lower part of the zone of *Globorotalia fohsi fohsi* (now N10, Middle Miocene, about 13 m.y. old). These figures give the rather wide age band of 9.5 million years in which the La Cira Formation could have been deposited. Hopping wrote (1967: 42) of the La Cira Formation that in the Middle Magdalena Valley area the interval of rocks concerned is developed in a fresh-water facies containing no other fossils. This statement ignores the macrofossil fauna entirely.

MUGROSA FORMATION. Van der Hammen (1961: 106), in common with Pilsbry & Olsson's (1935) work on the molluscs, dated this formation as Middle Oligocene (approximately Late Oligocene by modern terminology). Hopping (1967: fig. 10) sheds no direct light on the problem. He showed the La Cira Formation underlain by the 'A–B Sands' about which he gave no further information. These are presumably the 'A' zone of the Colorado Series, which is separated from the 'B' zone of the Mugrosa formation by the Mugrosa fossil horizon (Wheeler 1935: 32–33). These two bands are not separated in Hopping's diagram, but it seems likely that the Mugrosa fossil band would lie somewhere below the base of the zone of *V. rotundiporis* (i.e. below the top of the zone of *G. ciperoensis ciperoensis*, Zone P22). This would place the Mugrosa fossil horizon within the Oligocene.

Although de Porta (1974: 426) gave the age of the Mugrosa Formation as Upper Eocene to Oligocene, it appears that this conclusion was still based partly on Pilsbry & Olsson's molluscan evidence as well as newer palynological work. He suggested that van der Hammen (actually published 1961, but quoted by de Porta as 1958, appearing in 1960) had shown that the lower part of the Mugrosa Formation was the equivalent of the upper part of the San Fernando Formation, which had been placed in the zone of *Verrucatosporites usmensis* (Germeraad *et al.* 1968: fig. 18). This zone is thought to coincide with the Upper Eocene and may include small amounts of both Middle Eocene and Lower Oligocene (Germeraad *et al.* 1968: 244; fig. 15). Part of the Esmeraldas Formation, whose topmost bed is the Los Corros fossil horizon, is also said to lie within this zone. Although van der Hammen (1961: 97) deals with the San Fernando Formation, he does not refer to any correlation between it and the Mugrosa Formation. In addition, de Porta (1974: 496–500) discussed four different usages of the term San Fernando Formation, with ages ranging between ? Upper Eocene and ? Pliocene. In any case, the Mugrosa fossil horizon is at the top of the Mugrosa Formation, and therefore, even if the correlation between these two formations were correct, is likely to be distinctly younger than the zone of *V. usmensis*. In view of all these somewhat convoluted correlations, it must be concluded that the above work provided no satisfactory age determination for the Mugrosa molluscan fossil band.

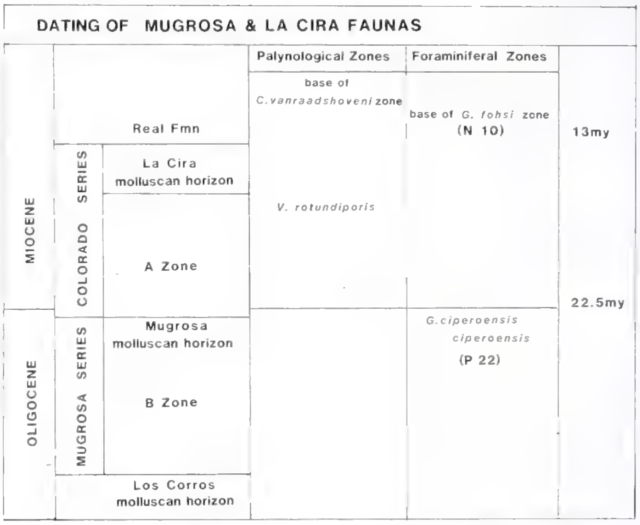

DATING OF MUGROSA & LA CIRA FAUNAS
Palynological Zones
Foraminiferal Zones
MIOCENE
OLIGOCENE
COLORADO SERIES
MUGROSA SERIES
Real Fmn
La Cira molluscan horizon
A Zone
Mugrosa molluscan horizon
B Zone
Los Corros molluscan horizon
base of C. vanraadshoveni zone
V. rotundiporis
base of G. fohsi zone (N 10)
G. ciperoensis ciperoensis (P 22)
13my
22.5my

Fig. 445 Dating of Mugrosa and La Cira molluscan faunas. Correlation chart showing inferred relationship between molluscan-bearing strata and palynological zones, and hence with planktonic foraminiferal zones. The La Cira molluscan horizon lies somewhere within the Zone of *Verrutricolporites rotundiporis*, which in turn lies between N1 and N9. The base of the Zone of *Crassoretrilites vanraadshoveni* is thought to be rather younger than the La Cira fauna. The palynological evidence for dating the Mugrosa fauna is less satisfactory and gives an older age than is suggested by the molluscan evidence (see Fig. 3, p. 171).

LOS CORROS FAUNA, TOP ESMERALDAS FORMATION. The bulk of the Esmeraldas Formation lies within the zone of *Retitricolporites guianensis* and the overlying zone of *Verrutricolpites usmensis*, according to Germeraad *et al.* (1968: fig. 17, section 2, Rio Lebrija). The top of the Formation, which yielded the Los Corros molluscan fauna, is not shown and is therefore presumably younger than the *V. usmensis* Zone which, as shown above, is mainly Upper Eocene but probably also including small amounts of both the Middle Eocene and early Oligocene (Germeraad *et al.* 1968: 244; fig. 15).

The Los Corros molluscan fauna is therefore, on palynological evidence, more likely to be of some unspecified Oligocene age than to be late Eocene.

San Juan de Rio Seco fauna (Anderson 1928)

There is some question about the horizon and position of this locality. Anderson (1927, 1928) thought it was in the coal-bearing Guaduas Series, and gave no precise locality. Butler (1939) suggested that it was not part of the Guaduas Series and proposed the name '*Corbula hettneri* Horizon' for these strata. He placed Anderson's locality at km 106 on the Bogotá to Cambao highway (K 106), but without providing supporting evidence. He repeated this conclusion (1942), which was later accepted by de Porta (1965: 37; 1966: 168, 173) who assigned the *Corbula hettneri* horizon to his new Santa Teresa Formation (1965). In neither of his papers did

Butler produce any adequate explanation of how he came to decide that Anderson's locality lay near K 106. Butler commented (1939: 99) that he had not observed Guaduas coal nearby. His section showed the *Corbula hettneri* horizon outcropping near the core of a syncline, presumably that now known as the Guaduas–Jurusalen syncline. His map (1942: 173) showed K 106 some 7 km NE by N of San Juan de Rio Seco.

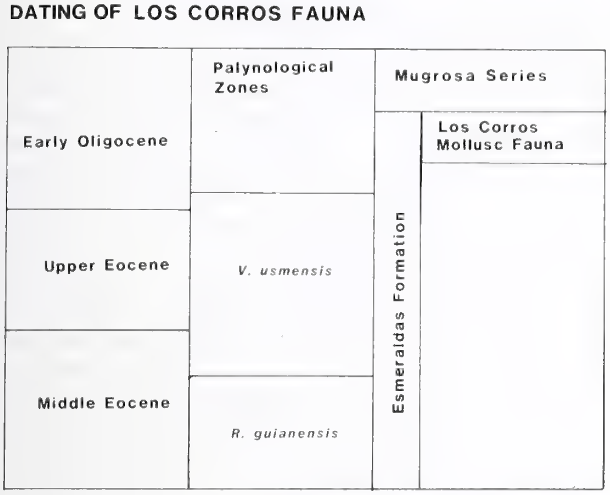


Fig. 446 Dating of Los Corros molluscan fauna. Correlation chart showing this fauna as being probably of some unspecified age later than the palynological Zone of *Verrutricolporites usmensis*, with the Zone of *Retitricolporites guianensis* as being distinctly older.

Anderson (1927: 599) regarded his fauna, collected by Downs McCloskey and Thomas Wark, as coming from the Guaduas Series. These he described as coal-bearing and carbonaceous beds, developed extensively in the Upper Magdalena Valley. He stated (1927: 604) that beds on Rio Sogamosa and upper tributaries of Rio Colorado (Middle Valley), and at San Juan de Rio Seco (Upper Valley), had yielded a fauna including *Ampullaria guaduasensis*, *Melanella magdalensis*, *Cyrena karsteni*, *Corbula hettneri* and numerous plant remains. This now appears to be a mixture of faunas from the two regions (see below). He also mentioned that similar beds and faunas were to be found a little to the east of Girardot. He argued (1927: 603) that the Guaduas series was Eocene, chiefly because of its stratigraphical position above the Guadalupe (of known Cretaceous age) and beneath presumably Miocene strata. He regarded (1927: 603, 1928: 13) the occurrence in Venezuela of similar coal-bearing beds which contained Eocene foraminifera as supporting his Eocene date for the Guaduas Series. Anderson had no palaeontological evidence for correlating his fossil locality of San Juan de Rio Seco with the true Guaduas Series.

The fauna from some 300 km further north in the Rio Sogamosa region of the Middle Valley of Rio Magdalena which Anderson referred to is likely to be from one of the horizons yielding the faunas later described in Pilsbry & Olsson (1935). The names in Anderson's list (1927: 604) quoted above are *nomina nuda*, and some were never to be formally described by him. He listed the following fauna as occurring in the Middle Valley (1928: 12): *Melania, Ampullaria, Corbula* and *Cyrena*. Later on the same page he listed the fauna from the Upper Valley at San Juan de Rio Seco (*Melanella karsteni* etc., see below). His reference to *Melania* is here interpreted as *Hemisinus*, whilst his *Cyrena* might well have been a reference to *Sogamosa cyrenoides* Pilsbry & Olsson. Both of these genera belong to families which are present in the Middle Valley faunas but not known from San Juan de Rio Seco.

Anderson also described in the same paper (1928) a large number of Colombian marine molluscs which were indisputably of Palaeogene age. He presented no evidence connecting the strata, from which these marine taxa were obtained, with the non-marine beds.

Anderson's type specimens are in CAS. These, and also a large sample (CAS 31695) have been re-examined. The latter yielded several hundred specimens of *Pachydon hettneri* (Anderson) and, in a separate container from possibly a different rock band, a few dozen examples of *Pachydon cebada* (Anderson). In this sample only three additional gastropods were found: unfortunately all were small and too poorly preserved even for superfamilial determination.

All the labels with the collection read 'from near San Juan de Rio Seco, East border of the Upper Valley of the Magdalena River, Colombia, from the lower part of the Guaduas Beds, not far from the horizon of the coal veins'. No additional information about Butler's (1939) views on this locality is present with the collection. It seems very unlikely that Butler ever saw this material.

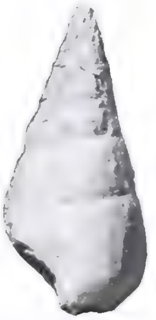


Fig. 447 *Melanella karsteni* Anderson (1928). CAS 2722; holotype. Probably from the Miocene Santa Teresa Formation, at km 106 on the Cambao to Bogotá Highway; originally described as being from the Eocene Guaduas Beds near San Juan de Rio Seco; × 4.

Fauna from San Juan de Rio Seco, described by Anderson (1928).

original determinations	**revised determinations**
Melanella KARSTENI Anderson v (Fig. 447)	Family indeterminate, possibly Littoridininae
Ampullaria GUADUASENSIS Anderson v	*Verena guaduasensis* (Anderson)
Corbula HETTNERI Anderson v	*Pachydon hettneri* (Anderson)
Corbula CEBADA Anderson v	*Pachydon cebada* (Anderson)
Corbula scheibei Anderson v	partly *P. cebada*, partly indeterminate *Pachydon*.

Pachydon is characteristic of the Pebasian and associated faunas. *Pachydon hettneri* also occurs in the La Tagua fauna, which has several species in common with the Pebasian. *Pachydon cebada* (Anderson), see p. 311, is a senior synonym of *Corbula abundans* Pilsbry & Olsson (1935), which is common in the La Cira fauna of the Middle Magdalena Valley. The holotype and only specimen of *Verena guaduasensis* (p. 256) is decorticated and lacks sculpture. Its shape and size is reminiscent of the living Brazilian type species, *V. crenocarina* (Moricand), which is represented by extinct subspecies in the La Cira fauna.

On this new interpretation of the molluscan palaeontological evidence, it is clear that there is a reasonably strong correlation between the San Juan de Rio Seco, La Cira and La Tagua faunas. It seems probable that all three are more likely to be early Miocene than late Oligocene.

Los Corros fauna, Middle Magdalena Valley (Pilsbry & Olsson 1935)

This is the oldest of the three thin but persistent fossil horizons with non-marine molluscan faunas described in Pilsbry & Olsson (1935) from the east side of the Middle Magdalena Valley. It contains no species common to the faunas dealt with herein. However, some consideration of it is appropriate because of its stratigraphical position below the Mugrosa and La Cira Formations. Current usage (de Porta 1974: 228, 380) still follows the views of Pilsbry & Olsson in regarding the Los Corros fossil horizon as the uppermost part of the Esmeraldas Formation and as being Middle to Upper Eocene in age. De Porta's dating was based not only on the molluscan evidence, but also on the palynological evidence discussed above.

Pilsbry & Olsson's type specimens are in ANSP and some of them have been re-examined. From their text, it is clear that at least some material remained in private collections, including that of Olsson.

original determinations	**revised determinations**
Hemisinus (Basistoma) CORROSENSIS Pilsbry & Olsson v	*Hemisinus* (s.str.) *corrosensis* Pilsbry & Olsson
Potamides MCGILLI Pilsbry & Olsson	*Potamides* (s.lat.) *macgilli* Pilsbry & Olsson
DIPLOCYMA WHEELERI Pilsbry & Olsson v	no change
Diplocyma SUCIONIS Pilsbry & Olsson	no change
SOGAMOSA CYRENOIDES Pilsbry & Olsson	no change

The Los Corros fauna thus consisted of five new species. *Diplocyma* was assigned to the Potamidinae and *Sogamosa* to the Corbiculidae. This small assemblage would have lived in water of low salinity, or fresh. Potamidinae tolerate brackish conditions, but the Thiaridae (of which *Hemisinus* is a member) are virtually restricted to fresh water. The Corbiculidae also live mainly in fresh water but are sometimes estuarine, and larger shells may be washed out to sea (Keen 1971: 111).

Pilsbry & Olsson's dating of the Los Corros fauna as Eocene was based on very weak evidence. They (1935: 7) thought that *Tympanotonus lagunitensis* (Woods) from the Saman Eocene of western Peru belonged to their new genus *Diplocyma*. However, the type series of this species (Sedgwick Museum, Cambridge), originally described as *Potamides lagunitensis* by Woods (1922: 90; pl. 11, figs 10–12) from the Eocene Lobitos Formation of the Pacific coastal region of Peru, appears to lack the strong opisthocyrt collabral folding of the early whorls of *Diplocyma*. The adult sculpture is rather simple and consists of two spiral rows of tubercles spaced at about twelve to the whorl: this in no way resembles the sculpture of either of the Los Corros species assigned to *Diplocyma*. The apertural features, in common with those of *Diplocyma*, are unclear.

Pilsbry & Olsson compared none of their other new taxa with species occurring elsewhere. Their argument that the Los Corros was Eocene also appears to have rested on the fact that marine Upper Eocene rocks were very widespread in the coastal region of northern Colombia. They therefore advanced the proposition (1935: 7) that it was reasonable to believe that the non-marine equivalents of these rocks should occur in the Tertiary embayments so well exemplified by the deposits of the Magdalena Valley. Clearly this argument cannot be taken seriously, either as evidence for the correlation they suggest, unsupported by any species in common, or, for that matter, of a physical connection at that time between the basins in which these different sediments were laid down.

There appears to be virtually no palaeontological evidence for dating this small fauna. None of the taxa present have been found elsewhere. In addition, none show any particular resemblance to those occurring either in the overlying Mugrosa and La Cira or at San Juan de Rio Seco (Anderson 1928). At present, *Potamides* is a very loosely defined, and hence long-ranging, genus with a living type species. The identification of *Hemisinus* seems reasonably sound. The first occurrence of the genus cannot be pinpointed with any accuracy, however, as arguments as to the ages of most records tend to be circular. Its type species is Recent, and at the present day the genus occurs both in the Caribbean region and in South America; *H. corrosensis* is not dissimilar from several of these living species. The inference from this is that the Los Corros fauna might well be younger than originally supposed. The palynological evidence can be interpreted as suggesting that the age is probably early Oligocene rather than Eocene. What little is known of the molluscs would not be in disagreement with such a conclusion.

Mugrosa Fauna, Middle Magdalena Valley (Pilsbry & Olsson 1935)

original determinations	**revised determinations**
Hemisinus (Hemisinus) SIGMACHILUS Pilsbry & Olsson (Rio Llano, Block 10S–11E) v	*Hemisinus sigmachilus* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) HOPKINSI Pilsbry & Olsson (near El Centro)	*Longiverena eucosmia* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) EUCOSMIA Pilsbry & Olsson (well 660, depth 1803–1815) v	*Longiverena eucosmia* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) LAPAZANA Pilsbry & Olsson (near El Centro, 16S–8E)	*Longiverena eucosmia* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) MUGROSANA Pilsbry & Olsson (Rio Llano) v	*Longiverena eucosmia mugrosana* (Pilsbry & Olsson)

The Mugrosa fauna is thus reduced to two genera, both with living type species, of the fresh-water Thiaridae, each represented by a single species, one with a distinct subspecies. Three synonyms of *Longiverena eucosmia* are recognized above. In the overlying La Cira fauna two further synonyms of this species are thought to occur, *L. lacirana* (Pilsbry & Olsson), and more doubtfully the poorly preserved *L. waringi* (Pilsbry & Olsson). Most of these synonyms are known only from their (mainly different) type localities. Both *L. hopkinsi* and *L. lapazana* were collected from near El Centro by Wheeler and may well have been found together, and their type illustrations certainly show them to be very similar. It is suggested here that the variation that occurs in these *Longiverena* is almost certainly only of local significance. *L. eucosmia* is also recognized as occurring in the Pebasian of Iquitos

(*Semisinus peyeri* de Greve, 1938) and in the Loyola Formation of the Cuenca Basin (*Hemisinus peyeri dickersoni* Palmer, *in* Liddle & Palmer 1941). In addition, the very similar *L. colombiana* sp. nov. (p. 249) is described from the La Tagua fauna. *Hemisinus sigmachilus* is a smooth species, based on a broken specimen; it is similar to a *Hemisinus* occurring in the Mangán Formation of the Cuenca Basin, but the lack of distinctive characters makes positive recognition unwise. Similar species are found living.

Pilsbry & Olsson (1935: 8, 13) suggested that some of the Mugrosa Formation *Hemisinus*, such as *H. mugrosana*, were closely related to the group of species in this genus described by Brown & Pilsbry (1914) and by Cooke (1919) from the Antiguan and Cuban Oligocene. *H. antiguensis, H. latus* and *H. siliceus* were described from Antigua by Brown & Pilsbry (1914). Their illustrations of the first-named (1914: pl. 9, figs 1, 3, 5, 6) are of blocks of rock crowded with shells not showing any generic characteristics. The sculpture appears to be of numerous, close-set, opisthocyrt collabral ribs, whilst (1914: 210) two or three spiral cords are said to be present above the lower suture. This sculpture is not similar to that occurring either in *L. mugrosana* or in any of the other Magdalena Valley *Longiverena* discussed herein. *H. siliceus* is a typical, smooth *Hemisinus*. *H. latus* also appears to be smooth, but its type illustration (1914: pl. 9, fig. 4) does not show the aperture clearly so its generic determination cannot be confirmed.

Cooke (1919: 117–120; pl. 3) described several Cuban and Antiguan species which he assigned to *Hemisinus*. They belong to a mixture of genera. His illustration of *H. siliceus* (1919: pl. 3, fig. 3) is definitely of a smooth *Hemisinus*. His figures of *H. antiguensis* are not necessarily correctly identified and may not all be of one species: none resembles the Colombian specimens. None of the other species belongs to either *Hemisinus* or *Longiverena*. Two of his species, *H. costatus* and *H. bituminifer*, which Pilsbry & Olsson (1935: 13) compare with *L. mugrosana*, are misidentified at superfamilial level: both belong to the Epitoniidae, a fully marine family.

Hence this correlation with the Antiguan and Cuban Oligocene, which has never been challenged before, and is quoted by de Porta (1974: 425), must now be considered worthless. The molluscan evidence for the age of the Mugrosa Formation now rests on the two species recognized above. Their occurrences elsewhere are all in rocks now thought to be no older than Miocene. The recognition of *L. eucosmia* in the La Cira Formation suggests that the Mugrosa is not much older.

La Cira fauna, Middle Magdalena Valley (Pilsbry & Olsson 1935)

Fourteen molluscan species were all described as new by Pilsbry & Olsson from the La Cira formation of the Middle Magdalena Valley. Wheeler (1935: 34) gave no details of the several fossil beds he encountered. From the rather sparse locality data, coupled with information on the different collectors (Pilsbry & Olsson 1935), it would seem that at least five minor, and apparently almost mutually exclusive, faunal associations are present (see below). The degree of overlap is not known. To give one example, the type locality of *Potamopyrgus laciranus* was quoted (1935: 9) as near Zopffs, La Cira district. They wrote that it occurred at many other localities in the La Cira district, being quite abundant in the La Cira haematitic sandstones with *Corbula abundans* and *C. magdalensis*. Whether any of these three species occur with any others is not entirely clear from the remainder of their paper.

All species listed below were described as new by Pilsbry & Olsson (1935). Authors' names are therefore omitted from the first column. Omission of authors' names from the second column implies no change in nomenclature, either at generic or specific level.

original determinations	**revised determinations**
Hemisinus (LONGIVERENA) WARINGI	*Longiverena* cf. *eucosmia* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) LACIRANA	*Longiverena eucosmia* (Pilsbry & Olsson)
Hemisinus (Verena) AVUS v	*Verena crenocarina ava* (Pilsbry & Olsson)
Hemisinus (Verena) LAEVICARINA v	*Verena crenocarina ava* (Pilsbry & Olsson)
Hemisinus? GRACILLIMUS	family uncertain
Potamopyrgus LACIRANA v	*Dyris lacirana* (Pilsbry & Olsson)
Triplodon LATOURI	*Diplodon (Ecuadorea) latouri* (Pilsbry & Olsson)
Diplodon (Rhipidodonta) OPONCITONIS	*D. (R.) oponcitonis*
Monocondylaea? MARSHALLIANA	*M.? marshalliana*
Anodontites LACIRANA	*A. lacirana*
Mytilopsis CIRA	*Mytilopsis scripta* (Conrad)
Corbula (Corbula) ABUNDANS v	*Pachydon cebada* (Anderson)
Corbula (Erodona) MAGDALENSIS v	*Pachydon cebada* (Anderson)
Ostomya colombiana	*Guianadesma colombiana* (Pilsbry & Olsson)

Comparatively few of the above species have been studied herein. The naiades, for instance, have been omitted because they are not comparable to species found in either the La Tagua or the Pebasian faunas. From references to the La Cira fossil band (Wheeler 1935, Butler 1939, 1942, de Porta 1966), many of these species would seem to be both abundant and widespread. These authors comment on the poor state of preservation of most fossils seen in the field. This explains the paucity of material in institutional collections. The following associations are recognized herein:

(1a). Near Zopffs, La Cira district (Waring Colln). *Dyris lacirana, L. eucosmia* (as *H. (L.) waringi*), *V. crenocarina ava* (as *avus*).
(1b). 7700N–4600W, Station West of Zopffs (Waring Colln). *Hemisinus? gracillimus*.
(2a). Haematitic sandstone near La Cira (? Waring Colln). *Dyris lacirana, Pachydon cebada* (as both *C. abundans* and *C. magdalensis*).
(2b) Near La Cira, square mile 1N–9E (Wheeler Colln). *L. eucosmia* (as *H. (L.) laciranus*).
(3) Rio Oponcito, near Guanabanas (Ollson & La Tour Colln). *V. crenocarina ava* (as *laevicarina*), *T. latouri, D. (R.) oponcitonis, M. marshalliana, A. lacirana, M. cira, G. colombiana*.

These different associations, collected by different people from different places, immediately raise the possibility that the concept of the La Cira fossil band, occurring at the top of what is nowadays referred to as the Colorado Formation, is a gross over-simplification of the situation. The presence of *L.*

waringi in (1a) suggests that *L. eucosmia* does indeed occur at an horizon other than in the Mugrosa Formation. In (2b), this species occurs by itself: as it does usually in the Mugrosa Formation. Association (3) contains all the fresh-water naiades reported from the formation. *Verena* is also thought to be exclusively fresh-water. However, both *Mytilopsis* and *Guianadesma* tolerate brackish conditions. Both (1a) and (2a) also contain a mixture of fresh and brackish water species. The only species at (2b) is the fresh-water *L. eucosmia*. The true generic, or even familial, position of *Hemisinus? gracillimus* is unknown, so nothing can be deduced about the facies of (1b), beyond the unlikelyhood of it being marine.

Pilsbry & Olsson (1935: 8) suggested that the La Cira Fauna was either Upper Oligocene or Lower Miocene. They argued that if the Mugrosa was Middle Oligocene, then the La Cira could not be older than Upper Oligocene, but there seems to be no good reason why the two have to be separated in age in this way. They apparently raised the possibility of a Lower Miocene age for the La Cira on the grounds that all the genera were still living. However, both *Hemisinus* and *Longiverena*, the only two genera occurring in the Mugrosa Formation, are also living.

There is comparatively little molluscan evidence as to the age of the La Cira associations. *Pachydon cebada* (Anderson) occurs in the San Juan de Rio Seco fauna of Anderson (1928), which also contains *P. hettneri* (Anderson) now recorded from La Tagua. A rather more tenuous link between Anderson's locality and the La Cira fauna is provided by the occurrence in both of not very well preserved specimens of *Verena* which bear some resemblance to the living type species *V. crenocarina*. If these two faunas are the same age as the La Tagua fauna, then they are most probably Neogene. Such an age is also suggested by the presence of *L. eucosmia*, which is here shown to occur in the Pebasian of the Amazon Basin and in the presumed Miocene of the Cuenca Basin, Ecuador. It should be stressed, however, that these correlations are based on a very few species in common, occurring, for the most part, in rather small faunas, which have a greater number of species not common to other faunas. The situation in the true Pebasian Basin is very different. There, the faunas are usually richer, and comparatively large suites of fossils may be found occurring at several localities which are not, admittedly, normally separated by such great distances.

Fauna of La Dorada district, Magdalena Valley (Butler 1942)

Butler's fauna (1942: 803), which he correlated with the La Cira, came from a short distance west of the junction of the Puerto Liévano and Puerto Salgar spurs of the Cundinamarca Railroad, perhaps 6 km NE of La Dorada. He stated that it was rich in bivalves and tentatively identified *Corbula*, 'possibly some *Hemisinus* forms, *Ostomya* sp.(?), and fish teeth'. He described the aspect of the fauna as being strikingly similar to that of his *Corbula hettneri* Horizon. However, Thiaridae, such as *Hemisinus* and *Longiverena*, have yet to be reported from that Horizon. Butler also felt that the general faunal aspect, lithological character and stratigraphical position of his locality were similar to that of the La Cira Formation in the Middle Valley. He stated that several fossil beds, rich in *Hemisinus*, occurred in creeks to the south of the railroad. Whatever doubts there may be about Butler's identifications, he must almost certainly have been dealing with a fauna containing both the brackish-water *Pachydon* and members of the fresh-water Thiaridae.

This fauna came from strata assigned by Butler (1942) to the Colorado Series. The immediately overlying beds in this area, which Butler regarded as part of the Honda Series, have since been named the La Dorada Formation (Wellman 1970: 2356–2357).

Fauna of Quebrada el Tabaco, Santa Teresa Formation (de Porta 1966)

De Porta listed a small fauna from this locality in the San Juan de Rio Seco district, although he was unable to establish the field relationship between it and Anderson's (1928) fauna. He (1966: 172) identified *Anodontites laciranus, Diplodon (Rhipidonta) oponcitonis* and *Hemisinus (Longiverena) waringi*, all of which were described by Pilsbry & Olsson (1935) from the La Cira Formation of the Middle Magdalena Valley.

These records show that non-marine faunas similar to those of the Middle Valley occur in the Upper Valley of the Magdalena. They also serve to confirm the molluscan palaeontological evidence that Anderson's fauna, which possesses species in common with both the La Cira and La Tagua faunas, is much younger than at first thought.

Inter-Andean basins, Ecuador

Reference should be made to the annotated bibliography of Ecuadorian geology (Bristow 1981), which postdates the Lexique (Bristow & Hoffstetter 1977).

Tertiary rocks outcrop over vast areas of the Oriente in Ecuador and there are reports of un-named non-marine molluscs occurring in them (Tschopp 1953). In contrast, the geology and palaeontology – particularly of molluscs – of the inter-Andean basins are comparatively well documented and have recently been reviewed in some depth (Bristow & Parodiz 1982). As is discussed below, the faunas are predominantly fresh-water, and the evidence of brackish conditions, though definite, is less than in most of the other faunas considered in the present work. Of particular importance is their report of a radiometric dating (1982: 8) of 19–20 million years for an andesite immediately underlying the Loyola Formation which has yielded by far the richest molluscan fauna. Their paper is divided into two parts. The first, by Bristow, describes the geology of all the Ecuadorean inter-Andean basins and reviews other non-marine deposits of neighbouring regions. The second part, by Parodiz, describes the molluscan faunas, which include many species known from earlier works. The large collections which Parodiz studied were made by Bristow and were split between the Carnegie Museum, Pittsburgh and BMPD. Other material in BMPD are some duplicates of *Sheppardiconcha bibliana* Marshall & Bowles, 1932, collected by Sheppard himself, who wrote on the geology (1934). The main part of Sheppard's collection, including type material, is in USNM. There are also in BMPD a few samples collected in 1926 by Professor C. Carrion, including some slabs of well-bedded marl with moulds of *Dyris* aff. *tricarinata* (Boettger) recorded by Bristow & Parodiz (1982: 16) as *D.* cf. *gracilis*, 'form' *carinata*. Palmer (*in* Liddle & Palmer 1941) described a large collection of fossils from the Cuenca Basin made by Liddle. These are now in PRI. There are thus fairly large collections of fossils from these basins in several institutions.

In the BMPD collections, a few taxa such as *Sheppardiconcha* *bibliana* Marshall & Bowles, *Diplodon (Ecuadorea) bibliana* Marshall & Bowles and *Neocorbicula cojitamboensis* (Palmer) are very common from several localities. In addition, at some horizons, there are bedding planes crowded with small hydrobiids. The three above-named species are indubitably of fresh water origin, though the hydrobiids could be from brackish water. However, of the thirty species recognized by Bristow & Parodiz (1982), most appear to be rare. Moreover, the vast majority of specimens are so poorly preserved that confident identification is seldom possible. These are not easy faunas with which to work.

No attempt is made here to revise the faunas described in Bristow & Parodiz fully. Species dealt with are those which are thought to occur in other faunas under consideration, or which appear to be closely related to relevant taxa. The result of this partial revision is that, with one exception, all the species from the Cuenca Basin said to occur in other faunas are now thought not to do so, having been misidentified in Bristow & Parodiz. The exception is *Aylacostoma peyeri dickersoni* (Palmer), now placed in the synonymy of *Longiverena eucosmia* (Pilsbry & Olsson), which occurs in both the Mugrosa and La Cira faunas of the Middle Magdalena Valley, Colombia as well as in the Pebasian of Iquitos.

In both the Mangán and Biblián Formations clays and shales alternate with arenaceous beds. Shales predominate in the Loyola succession. The fossil samples from the San Cayetano Formation are of moulds, mainly external, of small species on bedding planes in a creamy marl. The Tumbatú Formation samples are flat slabs of a monospecific shell limestone. The arenaceous beds of these inter-Andean basins are often crowded with fossils, usually belonging to only one of the few commonly occurring species. Such lithologies may well represent periods of extremely rapid deposition and have no exact parallel in any of the samples encountered from the Pebasian and La Taguan collections studied here.

Below, the faunas described in Bristow & Parodiz (1982) are reviewed in order.

Chota Basin, Tumbatú Formation

Bristow & Parodiz recorded (1982: 5, 40) only one molluscan species from the entire basin, which they identified both as *Liris minuscula* and *L.* aff. *minuscula* (Gabb). *L. minuscula* was originally described from Pebas, and the genus *Liris* has otherwise never been recorded from outside the Pebasian Basin. This material, BMPD GG19807–8, is regarded here as belonging to a rather variable, un-named, species provisionally assigned to *Liris* and dealt with in the systematic section herein (p. 208). Bristow & Parodiz also (1982: 40) referred to it as occurring in the San Cayetano Formation, but did not mention it in the appropriate stratigraphical section of their paper (1982: 16). No specimens to support this second record are present in BMPD.

Bristow & Parodiz did not formally suggest a date for the Tumbatú Formation, except that they thought the Pebas deposits were probably Upper Miocene to Lower Pliocene. Any implied correlation is obviously much weakened by the rejection of their specific determination. These authors also appeared to accept comments by Hall (*in* Bristow & Hoffstetter, 1977: 268) that similarities existed between bentonitic shales of the Tumbatú and Mangán Formations of the Cuenca Basin and also that similar lithologies occurred in the Arajuno, Curaray and Upper Pastaza Formations of the Ecuadorian Oriente. All these formations, including the Mangán, they assumed to be Upper Miocene. However, as is pointed out herein, there is no good palaeontological evidence yet available for dating these strata of the Oriente. Furthermore, correlation based on similar lithologies cannot be considered definite. The Tumbatú Formation is almost certainly Neogene, but evidence is lacking for any more precise age determination. *Liris* could be either from brackish or fresh water.

Cuenca Basin, Mangán Formation (dated as Upper Miocene by Bristow & Parodiz, 1982)

They (1982: 14) listed a fauna of two bivalve and five gastropod species from this formation. Species which they also report from the Loyola Formation are indicated thus *.

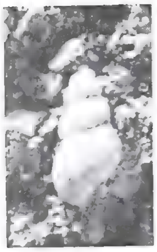
original determinations	**revised determinations**
Fossula cf. *derbyi* (von Ihering)	not revised
Neocorbicula cojitamboensis (Palmer) *	*Corbicula cojitamboensis* Palmer
Doryssa bibliana (Marshall & Bowles) *	*Sheppardiconcha bibliana* Marshall & Bowles
Aylacostoma browni (Etheridge)	*Aylacostoma* sp.
Aylacostoma sulcata (Conrad)	*Hemisinus* sp.
Neritina pacchiana Palmer *	accepted
Palaeoanculosa KENNERLYI sp. nov.	accepted

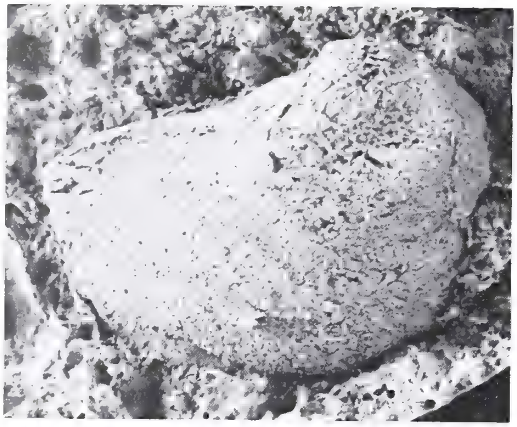
The ostracod *Vetustocytheridea bristowi* van den Bold (1976) was described from the Cuenca Basin, occurring in both the Mangán and Loyola Formations. Van den Bold did not clearly state the known range of the genus, but indicated that other species occurred in the early Miocene of the Gulf and Caribbean areas.

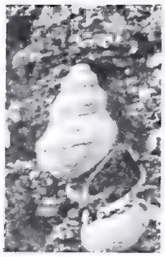
Although not in their faunal list (1982: 14), Bristow & Parodiz described and figured (1982: 41, fig. 16) a specimen which they identified as *Toxosoma eborea* Conrad, the only described species of the genus, which is known only from the Pebasian. Their figured specimen is not well preserved, but it shows clear signs of collabral folding, whilst *T. eborea* is smooth, and is almost certainly misidentified at generic as well as specific level. The specimen, BMPD GG19816, comes from the Loyola Formation (Loc. CRB 36) and not the Mangán Formation (CRB 26b) as they stated. It is presumably the source of their reference (1982: 18, table 2) to this species.

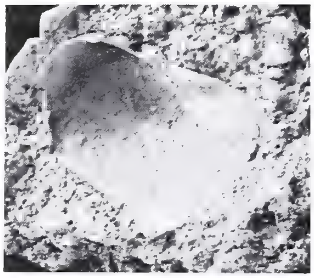
Both *Verena browni* (Etheridge) and *Hemisinus sulcatus* Conrad, which is herein assigned to the living species *H. brasiliensis* (Moricand) (see p. 244), occur in the Pebasian, but BMPD specimens from Mangán locality CRB 42, upon which Bristow & Parodiz' determinations were based, are now shown in the systematic section not to belong to these species. Their specimen of '*Aylacostoma browni*' from the Loyola Formation (GG19869) belongs to a different species, *Sheppardiconcha bibliana*. The Mangán fauna now appears to be endemic to the Cuenca Basin, with the possible exception of *F.* cf. *derbyi*, which they compared with specimens of unknown age from Rio Grande do Sul, Brazil (Bristow & Parodiz 1982: 14).

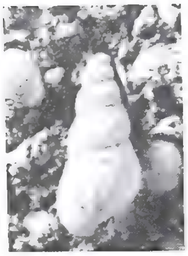
Bristow & Parodiz dated the Mangán Formation as Upper Miocene because it was separated by about 1800 m of sediments from the underlying Loyola Formation, which has several species in common and which they thought was Middle Miocene. In spite of the changes in identifications, it would appear that the Mangán Formation, yielding the


448


451a


450


451b


449

Figs 448–451 Miocene fossils from the Cuenca Basin, Ecuador; Bristow Colln. **448–450**, from well-bedded mudstone at Loc. CRB 11, Loyola Formation; all × 10. **448**, **449**, GG19814/1, 2; *?Dyris* sp., probably the species listed as *Lyrodes* sp. in Bristow & Parodiz (1982: 7). **450**, GG19814/3; indeterminate Hydrobiidae, *?Dyris* sp., probably the species identified as *Hydrobia ortoni* in Bristow & Parodiz (1982: 7). **451**, LL27817; *Corbicula (Cyanocyclas) cojitamboensis* Palmer. The specimen identified as *Erodona iquitensis* in Bristow & Parodiz (1982: 10, 31, but *not* that illustrated in their fig. 8); Loc. CRB 7, Basal Loyola Formation. Latex casts; a, external view of left valve, × 4 (interpreted as right valve in Bristow & Parodiz); b, internal view of left valve, × 2. See p. 315.

common *C. cojitamboensis* and *S. bibliana*, is likely to be fairly similar in age to the richer Loyola Formation. In an area of predominantly coarse sedimentation, the strata intervening between these two formations may well have been deposited fairly rapidly, so there is no real reason to postulate that the Mangán Formation is much younger than the Loyola.

Neritina can occur in fresh water, but is the only genus in this fauna which also has brackish and marine species. The remaining taxa are of exclusively fresh-water families.

Cuenca Basin, Azogues and Guapán Formations (dated as Middle Miocene by Bristow & Parodiz, 1982)

They (1982: 7, 11–12) recorded only three molluscan species from these formations. Both *Corbicula cojitamboensis* and *Aylacostoma* cf. *dickersoni* (=*Longiverena* cf. *eucosmia* herein) are known from other formations in the Cuenca Basin, whilst *Diplodon* sp. belongs to a genus common in the basin. All three indicate a fresh-water environment.

Cuenca Basin, Loyola Formation (dated as upper part of Lower Miocene by Bristow & Parodiz, 1982)

Of particular importance is the radiometric dating by Snelling (1974, unpublished report of Brit. Geol. Surv.; see Bristow & Parodiz, 1982: 8) of the Descanso andesite, which immediately underlies the Loyola Formation, at 19–20 million years. This is equivalent to Lower Miocene, late Aquitanian, Zone N5, and may be regarded as the maximum possible age for the formation.

The Loyola molluscan fauna is by far the richest from the Cuenca Basin. The biota includes plants (leaves, pollen and the almost ubiquitous *Chara*). Fish remains and the endemic ostracod *Vetustocythiridea bristowi*, which also occurs in the Mangán Formation, are also present. Bristow & Parodiz (1982: 11) argued that perhaps the best independent date for the Loyola Formation was the identification of the crab, *Necronectes proavitus* (Rathbun, 1919), originally described from the Gatun Formation of Panama which they stated was Middle Miocene. This age determination, however, must be revised in the light of new work. J. E. P. Whittaker (BMPD, unpublished report) has dated as probably N17 (Upper Miocene) the planktonic foraminifera obtained from Gatun clay, mainly extracted from mollusc shells provided by myself and the late W. P. Woodring (USGS). As the ages of many other formations in the same general area are frequently fixed by reference to the Gatun, they also may be due for revision. The potential age range for the Loyola Formation is thus widened to include the Upper Miocene. The presence of this crab, if correctly determined even at only generic level, occurring so far from its normal area of distribution, may be taken as evidence for some connection between the Cuenca Basin and the Panamic-Pacific marine province during the Neogene. (The crab was also recorded from other supposed Middle Miocene strata of the Caribbean area (Collins & Morris 1976: 125, *cum syn.*), but new information on the age of these latter occurrences is not available.)

Twenty-six molluscan taxa were listed from the Loyola Formation by Bristow & Parodiz (1982: 10).

original determinations	**revised determinations**
Diplodon (Ecuadorea) guaranianus biblianus (Marshall & Bowles)	*Diplodon (Ecuadorea) biblianus* (Marshall & Bowles)
Diplodon (Ecuadorea) BRISTOWI sp. nov.	accepted
Diplodon (Ecuadorea) liddlei (Palmer)	not checked
Monocondylaea azoguensis (Palmer)	not checked
Monocondylaea pacchiana (Palmer)	not checked
Monocondylaea sp.	not checked

original determinations	**revised determinations**
Anodontites olssoni (Palmer)	not checked
Pisidium sp.	not checked
Neocorbicula cojitamboensis (Palmer)	*Corbicula cojitamboensis* Palmer
Erodona iquitensis (de Greve)	*Corbicula cojitamboensis* Palmer
Ostomya cf. *fluviatilis* (H. Adams)	indet. ?bivalve
?Calliostoma sp.	not checked, determination extremely unlikely even at superfamilial level
Neritina LOYALAENSIS sp. nov.	accepted
Neritina pacchiana Palmer	accepted
Neritina sp.	not checked
Puperita aff. *sphaerica* (Olsson & Harbison)	probably indet. *Neritina*
Poteria (Pseudoaperostoma) bibliana (Marshall & Bowles)	not checked
Pomacea (Limnopomus) manco Pilsbry	not checked
Hydrobia ortoni (Gabb)	indet. ? Hydrobiidae
Lyrodes sp.	possibly *Dyris*
Potamolithoides biblianus Marshall & Bowles (*not* Conrad as stated)	accepted
Aylacostoma browni (Etheridge)	GG19869 from CRB 18 is possibly *Sheppardiconcha bibliana*. Note that Mangán specimens are *Verena*
Aylacostoma dickersoni (Palmer)	*Longiverena* cf. *eucosmia* (Pilsbry & Olsson)
Doryssa bibliana (Marshall & Bowles)	*Sheppardiconcha bibliana* Marshall & Bowles
Gyraulus sp.	not checked
Succinea sp.	not checked

The ostracod *Vetustocytheridea bristowi* van den Bold is also present. It is discussed briefly under the Mangán Formation, in which it also occurs (p. 339).

Specimen BMPD LL27817, from CRB 7, was identified in Bristow & Parodiz (1982) as *Erodona iquitensis* and is treated fully in the systematic section under *Pachydon iquitensis*, p. 315. It is here reidentified as *Corbicula cojitamboensis* Palmer, a common species in the Loyola Formation. Had its original identification been correct, this would have been the only record of Pachydontinae in the Cuenca Basin. LL27812, from CRB 26, identified as *Ostomya* cf. *fluviatilis* is also misidentified. It is not certain that it is a bivalve. *Puperita sphaerica* was described by Olsson & Harbison (1953) from the Pliocene of Florida. The greatly enlarged illustration (Bristow & Parodiz 1982: fig. 13) is barely recognizable as a neritinid, and certainly should not be taken as evidence for the presence of this particular species. Small Hydrobiidae occur quite commonly on bedding planes on blocks of gray shale (CRB 7, 11) along with small, uncommon, specimens of a corbiculid, which could be *Pisidium* sp. (s.lat.). The Hydrobiidae might be referrable to *Dyris* or *Lyrodes*, or both, but no specimens suggestive of the Pebasian *Dyris ortoni* (Gabb) have been seen (Bristow & Parodiz 1982: 39).

It thus becomes apparent that the molluscan fauna of the Loyola Formation is nearly all endemic. Possible exceptions are *Pomacea manco*, originally described from poorly preserved material from the Pachitea River Red Beds (Pilsbry 1944) and *Longiverena eucosmia* (Pilsbry & Olsson, 1935) known from the Mugrosa and La Cira fossil horizons of the Middle Magdalena Valley of Colombia and from the Pebasian of Iquitos. Three genera in the Loyola fauna, *Diplodon (Ecuadorea), Monocondylaea* and *Neritina* are each represented by three species: the quality of the material is such that it is difficult to be sure that these are all distinct.

This reassessment of the Loyola fauna shows that there is little direct palaeontological evidence as to its age. The radiometric age determination places a lower limit of Lower Miocene, whilst the presence of *Necronectes proavitus*, *Longiverena eucosmia*, and perhaps *Vetustocytheridea bristowi*, suggest that a post-Miocene age is highly unlikely.

As in the case of the Mangán Formation, the only family with some brackish and marine members is the Neritidae, though some species of *Neritina* are from fresh water. *Succinea* is a land pulmonate gastropod. All the other molluscs belong to exclusively fresh-water families.

Cuenca Basin, Biblián Formation (dated as lower part of Lower Miocene by Bristow & Parodiz, 1982)

The Biblián Formation has yielded (1982: 8) two species of molluscs, *Diplodon (Ecuadorea) bibliana* and *Sheppardiconcha bibliana*, both of which occur in the overlying Loyola Formation. Both species are indicative of fresh water. Its stratigraphical position below the Loyola, coupled with the occurrence of these two species, suggests that Bristow & Parodiz' age determination is likely to have been correct.

Loja Basin, San Cayetano Formation

This is the only other formation from which Bristow & Parodiz recorded fossil molluscs (1982: 16, 41). The specimens they cited as *Dyris gracilis* Conrad and 'form' *tricarinata* (Boettger) are dealt with here in the systematic section, under *Dyris tricarinata* (Boettger), p. 191. *Dyris gracilis* is very different from these San Cayetano specimens, which are preserved as external moulds on bedding planes of marl. The preservation is such that this determination must be slightly indefinite. Nevertheless, this is one of the least controversial records of Pebasian species from the Inter-Andean Basins of Ecuador. The age indicated by this gastropod cannot be determined closer than Neogene. *Dyris*, which is extinct, could be indicative of either fresh or brackish water.

In both the Loja and Malacatos Basins, there is said to be (Bristow & Parodiz 1982: 16) a conformable upward passage from the Trigal Formation to the San Cayetano Formation. The molluscs are recorded from the Loja Basin, but from the Malacatos Basin there is one Trigal sample said to contain the ostracod *Cyprideis stephensoni* Sandberg, 1964. On this occurrence, Bristow & Parodiz dated the Trigal Formation as Miocene. The species is recorded by van den Bold (1976: 6) as occurring in probably the uppermost Middle Miocene of Louisiana and the Culebra Formation of Panama. This identification, if correct, must be taken as indicating a likely Miocene age for the conformable San Cayetano Formation, and is also additional evidence for some connection between the Cuenca Basin and the Caribbean.

Oriente of Ecuador

Bristow (1981) should be consulted for further references.

Tschopp (1953: 2345) suggested that a Tertiary succession of up to 5000 m of rock laid down in fresh to brackish waters disconformably overlies a slightly eroded series of Cretaceous marine rocks in the Oriente of Ecuador. He dealt (1953: 2338, and stratigraphical sections in text-figs 4–6) with three formations which he regarded as Miocene, and from which, among other biota, he reported the presence at several levels of unnamed non-marine molluscs. Few details were given, but the clays of the Upper Arajuna (and possibly also the Upper Pastaza Formation – the wording is ambiguous) in the Vuano area were thought to have been laid down under conditions which allowed abundant plant life in rivers and swamps populated by turtles and fresh-water molluscs.

The overlying Curaray Formation of almost horizontal clays and sandstones exposed east of 76° 30′ W, between Rio Napo in the north and Rio Conambo in the south, contains lignitic seams and coaly black clays. It has yielded a fauna with crustacean and fish remains, turtles, crocodiles represented by both bones and teeth, as well as the remains of other unspecified vertebrates. Molluscs were an important element of the fauna and both arenaceous foraminifera and ostracods were also present. Of possible significance is the record of an ostracod similar to *Vetustocyprideis bristowi* van den Bold (1976) from this formation (Bristow 1973: 34; Bristow & Hoffstetter 1977: 108): the type strata of the species (*sensu stricto*) is the basal Loyola of the Cuenca Basin.

In his section on correlation, Tschopp (1953: 2339) briefly mentioned the similarities which he thought existed between these formations and those of other regions, but without giving detailed reasons. He suggested that both the Arajuno and Upper Pastaza Formations were comparable to the Honda of the Magdalena Valley of Colombia, whilst the Curaray showed affinities with the Colombian Miocene. It is difficult to assess his views as he did not suggest which of the numerous formations from widely different areas he had in mind when referring to the Colombian Miocene. Furthermore, the Honda Formation of the Upper Magdalena Valley is accepted as being of Miocene age by most authors: it is considered to be later than both the La Cira fossil band of the Middle Magdalena Valley and also its possible equivalent the *Corbula hettneri* Horizon of the Upper Valley (Butler 1942). Tschopp also suggested that part of the Contamana Group of Peru (Kummel 1948: 1254 *et seqq.*) might be the equivalent of all three of these formations of the Ecuadorean Oriente.

The age determinations that Tschopp gave for both older and younger Tertiary formations in the same region are all based on similar arguments. No palaeontological evidence was advanced as confirmation of the suggested ages. Some ostracods and arenaceous foraminifera were named, but were not used for correlation with strata whose ages had been established. The only definite limits on ages of the Tertiary sequence in the Oriente are set by the marine Cretaceous below and the present day above. It follows that without examining fossils from these formations, little can be deduced as to their age from Tschopp's account. The whereabouts of Tschopp's collection of fossils is unknown and he did not indicate whether anybody else had examined them. It seems reasonable to accept, however, that fresh to brackish sedimentation occurred in the Oriente of Ecuador during the Tertiary, probably whilst other formations considered herein were being deposited. Somewhat surprisingly, Tschopp made no reference to the Tertiary of the Cuenca and other inter-Andean basins of Ecuador.

Bristow & Hoffstetter (1977: 17 (fig. 3), 35, 107, 229) placed all three of the formations discussed here into the Upper Miocene, but the only new palaeontological evidence that they presented appears to be the reference to the ostracod *V.* aff. *bristowi* mentioned above. Campbell (1970: 20–22) also briefly reviewed Tschopp's work. He, too, concluded that there was no firm palaeontological evidence available with which these Tertiary deposits of the Oriente might be dated. His most significant observation was that they predated the late Andean orogeny: this argument is taken up below (p. 352) in discussing the palaeogeography.

Venezuela

No large faunas of Tertiary non-marine molluscs have been described from Venezuela, but there are several records, mainly of isolated species, which suggest a definite link between the present Caribbean coast and the Amazon Basin during the Neogene.

Late Cainozoic of Monogas

Palmer (1945) described nine species from east of La Llanera in the State of Monogas. Her discussion (1945: 7–8) showed that, in Norman Weisbord's opinion, her locality might be the equivalent of the Quiriquire Formation, whose type area appeared to be some 50 km distant from La Llanera. On these grounds they both concluded that the fauna was likely to be Pliocene, or less probably Pleistocene. Petzall *et al.* (1978: 529–530) date this formation as Lower Miocene. More importantly, although they mention the presence of non-marine molluscs, they do not refer to Palmer's fauna. It seems likely, therefore, that the latter is no longer regarded as being from this formation. Most of Palmer's species have not been revised herein as they have little bearing on the present work.

original determinations	**revised determinations**
Hyria trinitaria Maury (1925*b*)	not revised
Hyria WEISBORDI sp. nov.	not revised
Prodiplodon TIPSWORDI sp. nov.	*Diplodon tipswordi* (Palmer)
Castalioides laddi Marshall, 1934.	*Diplodon (Ecuadorea) bibliana* (Marshall)
Corbicula (Cyanocyclas) DESOLAI sp. nov.	not revised
Corbicula (Cyanocyclas) MONAGASENSIS sp. nov.	not revised
Ostomya MENCHERI sp. nov.	*Guianadesma sinuosum* (Morrison)
Asolene QUATALENSIS sp. nov.	not revised
'*Planorbis*' *LLANERENSIS* sp. nov.	not revised

The type occurrence of *Hyria trinitaria* is from Trinidad, said to be Pliocene (Maury 1925*b*: 235 (83); pl. 24 (13), fig. 2). *Castalioides laddi* Marshall (1934) was described from the Venezuelan Neogene as a new species and genus. *Castalioides* certainly appears to be a synonym of one of Marshall's numerous other naiad genera, *Ecuadorea*, which is now placed as a subgenus of *Diplodon*. *D. (E.) laddi* cannot be confused with the living *D. (E.) pazi* (Hidalgo). Parodiz (1969: 66) placed the former in the synonymy of *Ecuadorea bibliana* from the Miocene of the Cuenca Basin of Ecuador, with which I agree, even though the Cuenca Basin material is seldom well enough preserved to show all the details of shell sculpture.

Guianadesma sinuosum is dealt with in the systematic section, p. 319. It is living in the rivers of Guiana and Surinam and can tolerate slightly brackish conditions. Palmer (1945: 21–22) said her species was more similar to this living form and to those from the Pebas beds than to the older fossil species. Although true *Ostomya* was described from the

Pebasian, it has no close resemblance to *Guianadesma*. *Ostomya colombiana* Pilsbry & Olsson (1935) from the La Cira beds of the Middle Magdalena Valley of Colombia is here (p. 319) placed in *Guianadesma*, but it is too small and characterless to be usefully compared with the Venezuelan specimens.

It is not possible to give a precise age determination for this small fauna as only three out of the nine species present occur elsewhere. Although clearly Neogene, the further records, as discussed above, of those three species provide conflicting evidence as to the age.

Rutsch (1952), in a short paper, drew attention to the first occurrence of *Pachydon* of which he was aware from outside the Upper Amazon Basin. He had been shown by Leuzinger material in the collection of the Mene Grande Oil Company in Venezuela, and, on his return to Switzerland, had examined the collection from Iquitos in PIMUZ described by de Greve (1938). He concluded that well-preserved *Pachydon carinatus* Conrad definitely occurred in the 'La Puerta' Formation of Zulia and Miranda and that perhaps *P. cuneatus* Conrad occurred in the Yucales formation of the Santa Ines Group of Monogas and Guarico, as well as in Aragua. Petzall *et al.* (1978: 344) referred the La Puerta Formation to the Upper Miocene, whilst the Yucales Formation was regarded as invalid. Salvador (1964: 194) argued that the name, which had first been used by Leuzinger in Mene Grande Oil Company reports, might apply to various strata ranging in age from Oligocene or Lower Miocene up to Pliocene. No further references to the record of *P. carinatus* have been found, and although the records of *?P. cuneatus* are referred to by both Padrón (1956: 677–678) and by Tello (1975: 356), neither author added any new information. As well as the rather unsatisfactory nature of the original information, on both localities and stratigraphy, there is one further difficulty. Rutsch's paper, unfortunately, was unillustrated, so these most interesting records cannot be checked.

Jung (1965) described a marine fauna of 146 species from the Cantaure Formation of the Paraguana Peninsula, which is now dated as Miocene N8, approximately uppermost Lower Miocene (Peter Jung, personal communication). Jung identified a single shell as *Neritina* aff. *woodwardi* Guppy. This specimen, which is dealt with in the systematic section (p. 183), is tentatively reidentified as belonging to the Pebasian *Neritina ortoni* Conrad because of similarities in the form of the lower part of the columellar callus and inner lip region. These areas are very unusual in *N. ortoni* and serve to distinguish it from all other known western hemisphere species of *Neritina*. The much smaller marine genus *Smaragdia* is the only living genus in the family which is similar in this respect.

Macsotay (1968) described a few non-marine gastropod fossils from different formations in the State of Miranda. These were identified as *Amnicola ernesti* von Martens, *Hydrobia amnicoloides* Pilsbry, *Pachychilus laevissimus* (Sowerby) and *Strophocheilus ovatus iguapensis* Maury, none of which appear relevant to the present enquiry. In addition Macsotay described as new two species. *Hemisinus (Sheppardiconcha) picardi*, from the Siquire Formation, is not very well preserved, but appears to have some resemblance to *Sheppardiconcha lataguensis* sp. nov. (p. 237) from La Tagua. His *Hemisinus (?Hemisinus) barloventoensis* also occurs in the Siquire Formation, though its type locality is in the Cumaca Formation. It, too, is described from incomplete specimens and is here assigned to *Verena*: it has a striking resemblance to, but nevertheless appears to be specifically distinct from, *V. lataguensis* sp. nov. (p. 258), also from La Tagua. Both the Cumaca and Siquire Formations were considered to be either Middle or Upper Miocene in age (Petzall *et al.* 1978: 194, 587).

Argentina

Rich marine Tertiary molluscan faunas have been described from Argentina. In contrast, the non-marine faunas appear rather unimportant: many are summarized in Parodiz (1969). Von Ihering (1907: 461–468) commented on Late Cainozoic occurrences of a few, mainly living, species of *Strophocheilus, Chilina, Ampullaria, Diplodon* and *Corbicula*. He also referred to the living *Erodona mactroides* Bosc (as *Corbula*) occurring in marine beds of the Oligocene (nowadays considered to be almost certainly Neogene) but later restricted to brackish horizons. Comacho (1966) recorded *Succinea, Ancylus, Planorbis, Ampullaria, Lymnaea, Strophocheilus* and *Bulimulus* from the Quaternary of Buenos Aires Province. He also dealt with fossil occurrences of mainly living species including several (1966: 122–124) *Littoridina* (now probably all referrable to *Heleobia*) and to both *Erodona mactroides* and *Diplodon charruanus lujanensis* von Ihering (1907: 80), an extinct subspecies of a living species.

Aceñoloza & Toselli (1981: 186) referred to the presence of *Corbicula stelzneri, Diplodon* and *Ampullaria* in the San Lucas Formation in northwestern (sub-Andean) Argentina. It is in this region that any connection with the Amazon Basin would be most likely during the Neogene. Previously Windhausen (1931: 405) had referred to the occurrence of *Cyrena, Corbicula* and *Hydrobia* in the Estratos Calchequeños of the same region and quite probably in the same or equivalent strata. Parodiz (1969: 93; pl. 11, figs 2, 3) validated *Neocorbicula stelzneri*, previously a *nomen nudum*, from the Estratos Calchequeños, which he considered to be Middle Miocene. He gave no detailed synonymy, remarking that there was no guarantee that the numerous records of *Corbicula stelzneri* referred to the same species. These non-marine faunas contain Corbiculacea, not present in the Pebasian, and lack all the typical Pebasian genera. No previous author has, in fact, tried to compare them with the Pebasian, though Windhausen (1931: 403) drew attention to the bivalve occurrences in the 'Taterenda Formation' of the Rio Sapuru region of Bolivia (Mather 1922), which is discussed on p. 344.

The living Argentinian non-marine faunas are well known. Pilsbry (1911) described numerous species of his genus *Potamolithus*, which appears to be common in the eastern regions of the country and in neighbouring Uruguay. It has been assigned (Davis & Pons da Silva 1984) to the Lithoglyphinae of the Hydrobiidae, and is the only South American genus hitherto placed in the subfamily, which is known also living in North America. *Lithoglyphus* itself is living in Europe, where its fossil history is short, ranging back no further than the Pliocene. The endemic Pebasian genera *Eubora, Tropidobora*, and, with much less confidence, *Toxosoma* are herein regarded for the first time as probably belonging to the Lithoglyphinae (p. 214). This is the only possible connection between the Pebasian and Argentinian – either Tertiary or Recent – faunas that has come to light. So far, both the Pebasian and Argentinian records of Lithoglyphinae are equally difficult to explain, particularly as the group appears to have a very sparse fossil record world-wide.

So far, no other molluscan evidence has been found suggesting connection between the La Plata region and the Pebasian and related fossil provinces of Colombia and Ecuador. The fossil and living occurrences in Argentina of genera such as *Diplodon, Heleobia* and *Ancylus* cannot be considered significant in this context because they are so widespread. This lack of evidence for such a connection is accepted in view of the quality and quantity of work on the Argentinian Tertiary and Recent faunas. Workers such as von Ihering and Parodiz, to name but two, were well aware of the Pebas fauna, and it seems inconceivable that they would have failed to recognize the more obvious Pebasian elements, such as *Pachydon*. The Lithoglyphinae, discussed above, are comparatively small and have always presented a problem that few authors have been prepared to face. The hinge of *Erodona* shows that it is not closely related to *Pachydon*.

Bolivia

There are records from Bolivia of Tertiary beds crowded with poorly preserved *?Tellina*. *Tellina*, a marine genus, and *Pachydon* have certain similarities. The ventral commissure in both is frequently twisted and *Tellina*, like *Pachydon*, is usually smooth-shelled. In addition, it would be most unusual for *Tellina* to be found crowded together in the manner described by Mather (1922). The genus is a common constituent of inshore sands, and is comparatively rare as a fossil, because in these unstable environments most of the shells are fragmented and dispersed soon after death. When fossilized, *Tellina* usually occurs as one of the less common members of a diverse marine fauna. *Pachydon*, in contrast, is often found crowded together in a manner typical of non-marine deposits which are frequently rich in numbers of individuals but poor in numbers of species. It is just possible, therefore, that the two genera have been confused and that the occurrences detailed below represent some southward extension of the Pebasian deposits. Non-marine deposits of the north-west of Argentina, however, appear to contain a fauna which is completely unlike that of the Pebasian.

Mather described (1922: 729) the Taterenda Formation of probable Tertiary age and consisting of 3000 to 4000 ft (900–1200 m) of soft sandstones, shales, unconsolidated sands and clays occupying lowland areas. In a channel of Rio Sapuru on the west side of Sierra de Charagua (19° 27′ S, 63° 15′ W) (1922: 747 and text-fig. 17) he found a band crowded with bivalves and ostracods. The ostracods were identified as a single species of the long-ranging *Bythrocypris*. The bivalves were thought to be *Tellina* (1922: 750), but were too poor for positive identification, according to E. O. Ulrich (U.S. eological Survey, Washington). Mather also reported the presence of identical bivalves in similar strata north of Rio Grande, 3 miles (5 km) NW of Abapó (18° 45′ S, 63° 22′ W). Ahlfeld & Branisa (1960: 143) rename the Tatarenda Formation as Grupo estratos del Chaco (1960: 82); they also refer to the Estratos de Abapó and a distinct lithological horizon as Las Capas de Pelecypodos.

El Molino fauna, ? Palaeocene

Pilsbry (1939) described a small fauna, allegedly of Palaeocene age, from El Molino, NW of Potosi. It consisted of the following species:

Doryssa(?) ANDICOLA (pl. 9, figs 1a, b).
Planorbis MOLINO (pl. 9, fig. 3).
Planorbis sp. indet. (unfigured).
Corbicula DORMITATOR (pl. 9, fig. 2).
Pisidium sp. indet. (unfigured).

From the illustrations it appears that these fossils are not well preserved, but they are not similar to any of the species from the strata discussed herein, from countries further north. This material has not been reexamined by me. Parodiz (1969) dealt with the three specifically named taxa: he, too, did not attempt to revise Pilsbry's work.

CONCLUSIONS

Summary of systematic zoological and palaeontological results

This study is partly limited in extent by its original aim of describing the new fossil faunas from La Tagua and comparing them with the well-known faunas of supposed Pliocene age in the Pebasian Basin. The work has continued in these directions, even though it has, perforce, expanded to consider other fossil faunas including those of the Cuenca Basin, Ecuador and those previously thought to be of Palaeogene age from the Magdalena Basin of Colombia. In consequence, although efforts were made to borrow type material from other institutions, loans were restricted to species which, at the time, appeared to be strictly relevant to the original aims of the study. The result is that not all species occurring in the non-marine Tertiary of the northwestern quadrant of South America are dealt with as fully as those in the Pebasian and La Taguan faunas. The Corbiculacea, which are unknown in these faunas, are omitted entirely, whilst the Unionacea and Mutelacea, which are comparatively rare in these same faunas, are not covered in great detail.

The generic and suprageneric classification of the fossils seemed to be of vital importance to any revisory work. Considerable efforts have therefore been made to understand the classification and distribution of the living non-marine molluscan fauna of both South and Central America, efforts justified by the consequent increased knowledge of the relationship between the fossil faunas and those of the present day, both at the taxonomic level and as a basis for considering the palaeogeography and related topics such as migration routes. As part of the taxonomic work, dates and authorship of suprageneric taxa have been thoroughly revised. Those given here are often different from those quoted in the *Treatise on Invertebrate Paleontology* (**N**, Bivalvia; Cox *in* Moore 1969), whilst the major part of the volume on Gastropoda (**I**) has yet (1989) to appear.

Neritacea

The several nominal species of *Neritina* (*sensu lato*) described from the Pebasian are here united in *N. ortoni* Conrad, 1871*b*. A single specimen, figured under another name by Jung (1965) from the marine Miocene of northern Venezuela, is tentatively referred to it. *N. ortoni* does not closely resemble any other known fossil or Recent species from either South America or the Caribbean, and there must be some doubt about its generic or subgeneric determination. Certain features of its ventral surface resemble those of the marine genera *Velates* (Eocene) and the living *Smaragdia*. A single operculum, extracted from washings of matrix from Pichana, a Pebasian locality rich in *N. ortoni*, appears to lack the peg characteristic of both *Neritina* and *Smaragdia*. The operculum of *Velates* is unknown.

Rissoacea

Three subfamilies, Littoridininae, Lithoglyphinae (probably; see p. 214) and Cochliopinae, all belonging to the Hydrobiidae, are present in the Pebasian. The Littoridininae are by far the most important, occurring in all the other fossil faunas under consideration and with a widespread distribution throughout South and Central America at the present day (Taylor 1966).

LITTORIDININAE. Two extinct genera of Littoridininae are of importance, and were described by Conrad (1871*b*) from the Pebasian of Pichana. *Dyris* is distinguished from living *Heleobia* by spiral ribbing, sometimes confined to its early post-nuclear whorls, whilst *Liris* has axial folding. Taylor's (1966) assignment of both to the North American genus *Tryonia* is not followed here. Parodiz (1969) reduced the number of Pebasian species of *Dyris* from five to two, recognizing only *D. ortoni* (Conrad) for large, rather smooth, shells and *D. gracilis* Conrad (the type species) for those with strong, persistent, spiral ribbing. The examination both of type material and of comparatively large samples from several localities, some new, suggests that more rather than fewer species should be recognized at our present state of knowledge.

However, the ideas of both Parodiz and Taylor should be borne in mind when examining an unresolved taxonomic problem, which has not previously been reported. In a few of the specimens studied herein, either the spiral or axial sculptural elements are reduced, producing shells with morphology intermediate between *Dyris* and *Liris*. For the time being, both genera are retained as they are useful for groups of fossil species clearly distinct from any Recent species. The view is taken that an attempt to merge the two would only be justified as part of a complete revision of the subfamily. Any such revision would have to redefine many of the Recent genera with respect to their type species, and, in view of the misunderstandings which had arisen with both *Dyris* and *Liris*, should preferably involve re-examination of their type specimens too. A probably unnecessarily large number of generic names is available, and much of the variation in form may be owing to radiation in isolated basins. A possible example of this is afforded by the several genera described from Lake Titicaca (Haas 1955), the majority, or even all, of which could have been derived from a rather 'normal' *Heleobia*-like ancestor. This situation is somewhat analogous to the diversity shown by Thiaridae (*sensu* Wenz, 1939) in Lake Tanganyika. With these reservations in mind, it may be suggested that the living *Heleobia*, *Lyrodes* and *Pyrgophorus* may share the same common ancestry as *Dyris*. The type species of the living *Potamopyrgus* is from New Zealand: use of the name for South American species seems inappropriate.

Both *Liris* and North American *Tryonia* exhibit rather similar axial folding, and it is felt that this resemblance could also well be owing to convergence. There are no South American genera particularly resembling *Liris*: it, too, may well share common ancestry with *Dyris*. *Liris laqueata* Conrad, 1871*b*, the type species, proves to be a junior synonym of *Turbonilla minuscula* Gabb, 1869. An attempt is made to rectify the confusion caused by the two being regarded by all subsequent authors as very different species.

A species based on three specimens from the Pebasian of Canamá and described by Etheridge (1879) as *Assiminea crassa* is, following Kadolsky (1980), tentatively assigned to *Littoridina*, though its generic position is not fully understood.

Potamopyrgus laciranus (Pilsbry & Olsson, 1935) from the La Cira formation of the Magdalena Valley, Colombia, is placed in *Dyris*. Bristow & Parodiz (1982) recognized *Liris minuscula* (Gabb) in the Tumbatú Formation of the Loja Basin, Ecuador. Their identification of *Liris* is provisionally accepted, but their specific determination is not. The species, which remains formally undescribed, is the only probably true record of *Liris* from outside the Pebasian Basin.

The following species are described as new: *Dyris hauxwelli*, Pebasian, Pichana, Peru; *Dyris semituberculata*, La Tagua Beds, La Tagua, Colombia; *Liris acicularis*, Pebasian, Pichana, Peru.

LITHOGLYPHINAE. Davis & Pons da Silva (1984) assigned the living Argentinian fresh-water genus *Potamolithus* to the Lithoglyphinae: previously it had been classified rather unconvincingly in several unsuitable positions in the Rissoacea, mainly within the Littoridininae. The endemic Pebasian genera *Eubora, Tropidobora* and *Toxosoma* are herein also provisionally placed in this subfamily. The first two have obvious resemblances to *Potamolithus*, but have a strong siphonal notch lacking in both *Potamolithus* and *Mexithauma*. *Toxosoma* has always presented a problem because, unlike other known Hydrobiidae with the exception of *Hemistomia*, it possesses a columellar plait. However, there is no other family to which it seems more likely to belong. It has a strong resemblance to some species of *Drymaeus*, a South American tree snail of the Bulimulacea, but the much smaller *Toxosoma* has a shell whose structure and texture is quite clearly prosobranch and not pulmonate. The similarity between the two appears to be a remarkable example of homoeomorphy between two genera living in very different habitats.

Records of *Toxosoma* from the intermontane basins of Ecuador (Bristow & Parodiz 1982) are unfounded. It is suggested below (p. 353) that the presence of Lithoglyphinae in the Pebasian Basin is evidence that it had some fresh-water link with the La Plata region. It is felt, however, that too little is known about either the true geographical distribution or the geological history of this group for such evidence to be relied on to any great extent. *Lithoglyphus* itself is living in Europe, and other genera assigned to the family live in North America. From neither region is there evidence of it having an extensive geological record before the Pleistocene.

COCHLIOPINAE. The subfamily is distributed mainly in the Caribbean, Central America and the southern United States (Texas etc.). The present fossil record is the first from South America and may well be the first from anywhere of *Nanivitrea*, described living in Jamaica and Cuba. The only other South American record of the genus is of *Valvata kugleri* Forcart, 1948, described from Venezuela Recent and assigned herein to *Nanivitrea*. *Nanivitrea colombiana* from the La Tagua Beds of La Tagua, Colombia is described as new.

VITRINELLIDAE. At least two species of Vitrinellidae, both best assigned to *Vitrinella (Vitrinellops)*, are present in the Pebasian. This is, as far as is known, the first record of this marine family in non-marine strata. The embryonic shell appears to be of only half a whorl and is suggestive of lecithotrophic development. In contrast, all the embryonic shells of marine vitrinellids which have been examined suggest that a free-swimming veliger stage is normal in the family.

Cerithiacea

Following the views of Morrison (1954), the Thiaridae (*sensu* Wenz, 1939) are divided into dioecious Pleuroceridae, which includes the genus *Doryssa*, and the parthenogenetic Thiaridae, to which are assigned the Hemisininae. Parodiz (1969), following Morrison's apparently mistaken views on the shell features distinguishing the two families, placed numerous fossil species in *Doryssa*. All of those species with which the present study is concerned are now regarded as Hemisininae, which may be distinguished from Pleuroceridae by the presence of a basal apertural notch. *Doryssa* is no longer recognized as occurring fossil in north-western South America. For comparative purposes, the genus is discussed and illustrated (p. 230), with particular emphasis on its living type species, *Bulimus ater* Bruguière, from French Guiana.

HEMISININAE. The type species of the living genera *Basistoma, Hemisinus, Verena, Longiverena* and *Aylacostoma* and also the fossil *Sheppardiconcha* are described, and fairly extensive synonymies are suggested. *Sheppardiconcha* is considered to be particularly close to *Basistoma*. Shells of Hemisininae are almost invariably decollated, so that their early whorls cannot be studied using adult specimens. Embryonic shells, syringed from dead shells in the dry collection of BMZD, of all the living genera except *Aylacostoma* are illustrated. In all of these, the initial shell is hemispherical and develops into a loosely coiled planorbiform phase of little more than one whorl. After this, the shells of the various genera fairly rapidly develop their own characteristics, which in some cases, but not all, is very like that of the adult shell.

Most of the Recent genera and species of Hemisininae dealt with herein come from the southern and eastern parts of Brazil, whilst the fossil localities are all in the Upper Amazon Basin and from even further west in the Magdalena and Cuenca Basins and from La Tagua on Rio Caqueta. *Hemisinus* also occurs living in the Caribbean as well as eastern South America, and is known fossil from the Miocene of the Dominican Republic. The differences between the fossil and Recent distributions of the majority of these genera raise the possibility that they developed in the more westerly basins and spread to the eastern parts of the Continent following the breakdown of the drainage divide in the middle to lower Amazon which existed in the late Tertiary, according to the hypothesis of Kätzer (1903). These ideas, however, cannot be properly tested, as both the details of Recent distribution and the taxonomy (as witness the locality data and synonymies given herein) of the various taxa involved are not properly understood. Furthermore, our knowledge of their distribution is very much controlled by the fact that all the fossil deposits lie to the west, whilst their most suitable habitats at the present day occur in the east, where they are also possibly more accessible to the average collector, as opposed to the professional oil and survey geologists and geographers responsible for much of the fossil collecting.

In addition to the synonymizing of many nominal living species, the following taxonomic changes are suggested. *Hemisinus tuberculiferus* Conrad, from the Pebasian of Iquitos, Peru, is assigned to *Sheppardiconcha*. *Hemisinus sulcatus* Conrad, from the Pebasian of Pichana, Peru is assigned to the living *H. brasiliensis* (Moricand). *Hemisinus sulcatus* de Greve, *non* Conrad, from the Pebasian of Iquitos, is assigned to the living *H. kochi* (Bernardi). The majority of the species described by Pilsbry & Olsson (1935) from the Mugrosa and La Cira Formations of the Middle Magdalena Valley, Colombia, are placed in their species *Longiverena eucosmia*: *Semisinus peyeri* de Greve, from the Pebasian of Iquitos, and *Hemisinus peyeri dickersoni* Palmer, from the Cuenca Basin, Ecuador, are also placed in the synonymy of this species. *Purpura woodwardi* Roxo from the Pebasian of Três Unidos, Peru is assigned to the living *Verena crenocarina* (Moricand). Both *Hemisinus (Verena) avus* and *H. (V.) laevicarina* Pilsbry & Olsson, from the La Cira formation of the Middle Magdalena Valley, Colombia, are placed in *Verena crenocarina ava*. *Ampullaria guaduasensis* Anderson, from what is now thought to be the Santa Theresa Formation of the Upper Magdalena Valley, Colombia, is placed in *Verena*. *?Melanopsis browni* Etheridge, described from the Pebasian of Canamá, Peru, is also assigned to *Verena*.

The following new species are all described from the La Tagua Beds of La Tagua, Colombia: *Sheppardiconcha lataguensis, Longiverena colombiana* and *Verena lataguensis*.

Pulmonata

Only two species of pulmonate gastropod have been discovered in any of the fossil deposits dealt with herein. Both are from the Pebasian of Pichana, Peru.

ORTHALICACEA. *Bulimus linteus* Conrad, which was also recorded as occurring at Pebas by Boettger (1878), is now assigned to *Orthalicus*. The superfamilial name Orthalicacea is here used rather than Bulimulacea.

LYMNAEACEA. A single, minute, limpet-like shell, adhering to a broken fragment of a bivalve, was extracted from matrix from Pichana. It is provisionally assigned to *Hebetancylus*. This is thought to be the first fossil record of the genus.

Order Unionida ('Naiades': Unionacea and Mutelacea)

Following Parodiz & Bonetto (1963), the Unionacea, with glochidia larvae, and the Mutelacea, with lasidia – a distinction first noted by Ihering (1893) – are treated as separate superfamilies. The thicker and coarser outer prismatic layer of the shell observed in all Mutelacea examined herein is advanced as an additional distinction between the two. A table (p. 265) is provided giving references to members of these superfamilies described as occurring in the Tertiary of north-western South America. Neither superfamily is of importance either in the Pebasian or in the La Tagua Beds, though shell fragments are a noticeable feature at a few localities. This is in contrast to the present-day Amazon freshwater fauna, in which they, along with the Corbiculacea, are the most important bivalve groups, as in virtually all normal fresh-water faunas of the Tertiary and present day. Naiades form a significant part of the fauna both at some horizons in the Magdalena Basin Tertiaries and in the Cuenca Basin, where some beds are covered in *Diplodon (Ecuadorea) bibliana* (Marshall & Bowles, 1932). All naiades are truly fresh-water and there relative abundance is clearly of importance when assessing facies considerations.

*UNIONACEA.*The genus *Diplodon*, its living type species, *Diplodon ellypticus* Spix, 1827, and its various subgenera, in particular *Ecuadorea*, are discussed in some detail. Although a few species have been described from the Pebasian, only very juvenile shells have been extracted from BMPD collections from Pichana, Peru. A single specimen from La Tagua is identified as *Diplodon (Ecuadorea)* aff. *bristowi* Parodiz, a Cuenca Basin species known only by its holotype. This determination is too uncertain for stratigraphical conclusions to be drawn from it.

MUTELACEA. The genus *Anodontites* and the Pebasian species *Anodon batesi* Woodward, 1871, from Pichana, which is here placed in it, are both redescribed.

Dreissenacea

A reappraisal of the apparently largely ignored work of Andrussov (1897) shows the geographical and stratigraphical distribution of *Mytilopsis* to be very different from that suggested in modern works, including the *Treatise* (Keen, *in* Moore 1969). The genus is recognized as occurring in the European Eocene, but its present-day distribution in Europe is interpreted as the result of reintroduction by man. Its distribution in the western hemisphere from the late Oligocene onwards is of some importance when considering the palaeogeography of north-western South America, see pp. 279 and 352. Two species are recognized in the faunas under consideration, *M. scripta* (Conrad), originally described from the Pebasian, and the living Caribbean *M. sallei* (Recluz), for which an extensive synonymy is constructed (p. 280).

Mytilopsis has a very wide salinity tolerance, enabling it to withstand hypersaline conditions and apparently to migrate across seas: nevertheless, it is normally found in fresh to brackish water.

Corbiculacea

The superfamily is not dealt with herein, as it is absent from the Pebasian and the La Tagua Beds. Accounts of its occurrences elsewhere are given by Bristow & Parodiz (1982; Cuenca Basin, Ecuador), Pilsbry & Olsson (1935; Middle Magdalena Valley, Colombia) and Palmer (1945; Neogene of State of Monogas, Venezuela). Corbiculacea and *Pachydon* of the Corbulidae seem to be of inversely proportionate importance in the fossil faunas under consideration herein.

The superfamily is predominantly fresh-water. The Pisidiidae are apparently entirely fresh-water, but, as Keen (1971: 111) has pointed out, the Corbiculidae are also sometimes found in brackish water and shells of more robust species may even be washed out to sea and mingled with those of marine faunas.

Myacea (Corbulidae, Subfamily Pachydontinae)

Pachydon Gabb, 1869, of the Corbulidae, normally a marine family, is by far the most important genus of bivalve, both in numbers of species and of individuals, in the Pebasian. Its type species, *P. obliquus* Gabb, is highly inequivalve and with a strongly twisted commissure. At several localities, however, it occurs with other clearly congeneric species of less unusual appearance, which are almost equivalve. Such species, when occurring in other strata, have invariably been assigned to *Corbula*. In the present work, *Pachydon* is recognized as abundant in the La Tagua Beds, and at several levels (including the *Corbula hettneri* Horizon, of the Santa Teresa Formation) in the Upper Magdalena Valley, Colombia. It is absent from the Cuenca Basin: a single specimen from the Loyola Formation, identified by Bristow & Parodiz (1982) as *Erodona iquitensis* (de Greve) has proved on re-examination to belong to the rather common species *Corbicula cojitamboensis* Palmer. Fuller details of the distribution of *Pachydon*, possibly including Venezuela (Rutsch 1952) and the more remote parts of the Upper Amazon Basin (Willard 1966), are given on pp. 292 and 353.

Over a dozen species of *Pachydon* are now recognized. At some Pebasian localities, five or six morphologically distinct forms, with no individuals showing intermediate characters, may occur together: in consequence, their treatment as separate species seems fully justified. *Corbula abundans* and *C. magdalensis*, both of Pilsbry & Olsson, 1935, from the La Cira formation of the Middle Magdalena Valley, are placed in *Pachydon [Corbula] cebada* Anderson, 1928, from what is now thought to be the Santa Teresa Formation of the Upper Magdalena Valley. *Pachydon [Corbula] hettneri* Anderson, 1928, from the same locality occurs in the newly described La Tagua fauna.

Three other genera of Corbulidae, *Ostomya* Conrad, 1874*a*, *Guianadesma* Morrison, 1943, and *Pebasia* gen. nov. (p. 315) also occur, but much more rarely, in the Tertiary of north-western South America, and are dealt with below. All four of these genera are here placed in the Pachydontinae of Vokes, 1945. Their shell structure is consistent with membership of the Corbulidae.

Pebasia is described to accommodate a single species, *Pachydon (Anisorhynchus?) dispar* Conrad, 1874*a*, from the Pebasian. In Conrad's original description of this species, the left and right valves were confused. It is highly inequivalve with a pholadiform right valve and *Spondylus*-like left valve. It probably shares common ancestry with *Pachydon*.

Ostomya was described by Conrad, who confused its left and right valves, to accommodate a single, small, species, *O. papyria* Conrad, 1874*a*. The type specimens are lost, but the taxon is now redescribed from newly extracted specimens from matrix from Pichana, Peru (one of the localities from which Conrad's collection came). *Ostomya*, which has often been assigned to the Lyonsiidae, is here transferred to the Corbulidae: its shell lacks the nacreous layer characteristic of Lyonsiidae. The only two other species assigned by earlier workers to *Ostomya* are here transferred to *Guianadesma*. *O. mencheri* Palmer, 1945, from the Neogene of Venezuela, is regarded as a synonym of the living type species, *G. sinuosa* Morrison, 1943, from the Guianas. *O. colombiana* Pilsbry & Olsson, 1935, is also transferred to this genus.

Guianadesma Morrison, 1943, is here used both for *Himella* H. Adams, 1860, and for its replacement name, *Antecorbula* Dall, 1898. These are here treated as *nomina dubia*, being based on an unfigured type species whose type material is lost. *Guianadesma* and *Ostomya* may share common ancestry.

New taxa of Corbulidae described herein are the genus *Pebasia* (see above) and two species, *Pachydon ovalis*, La Tagua Beds, La Tagua, Colombia, and *Pachydon trigonalis*, Pebasian, Puerto Nariño (type locality) and Canamá.

Summary of stratigraphical results

This section is concerned mainly with two aspects of the findings detailed in the sections devoted to systematic palaeontology and to descriptions of localities and their faunas: the correlation between the faunas under consideration, and evidence from any source, molluscan or otherwise, on the age of these faunas.

The faunas of several Pebasian localities have been generally recognized as being basically similar to each other. However, hitherto there have been no very serious attempts to correlate the faunas of various regions of north-western South America with each other. One exception to this is the

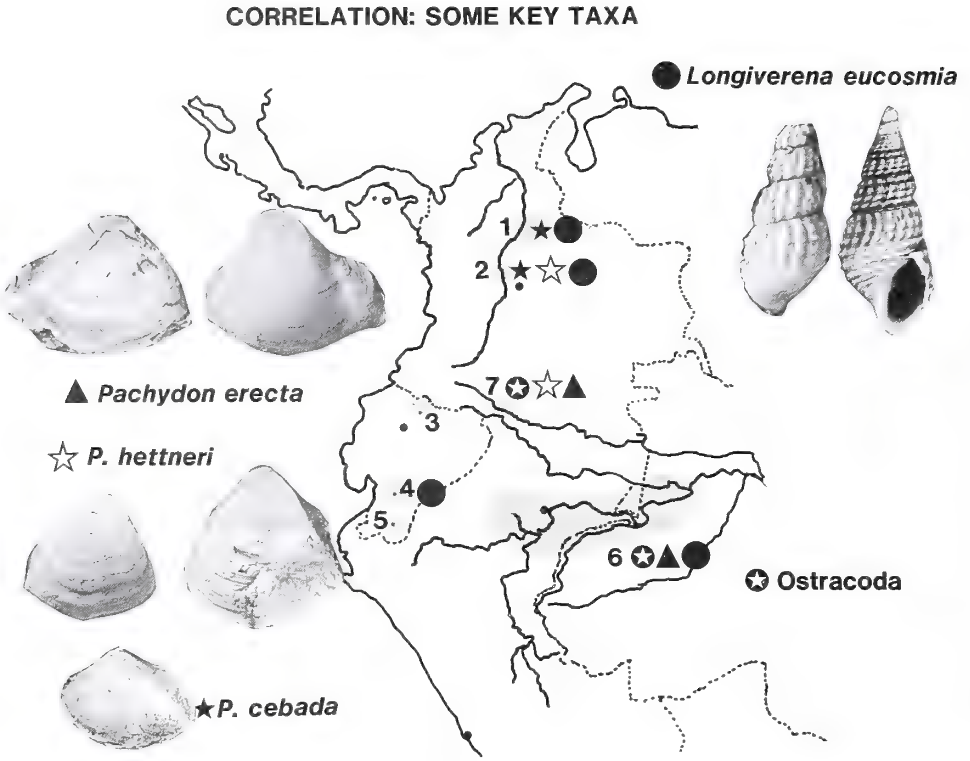


Fig. 452 Correlation: some key taxa. Diagram showing some of the more important links between molluscan species from the Mugrosa and La Cira faunas of the Middle Magdalena Valley (1), the Santa Teresa fauna of the Upper Magdalena Valley (2), both of Colombia; the Cuenca Basin of Ecuador (4); the classic Pebasian area of Peru and Brazil (6); and the La Tagua area (7). In addition identical ostracod species are known from both (6) and (7). (3) and (5) mark the Chota and Loja Basins respectively.

Pachydon erecta Conrad, left specimen from La Tagua, right from Canamá (Pebasian); *P. hettneri* (Anderson), left specimen from La Tagua, right from near San Juan de Rio Seco (2); *P. cebada* (Anderson), also from (2); *Longiverena eucosmia* (Pilsbry & Olsson), left shell from Mugrosa Formation (1), right from Iquitos (Pebasian) (6).

study of the faunas of the intermontane basins of Ecuador (Bristow & Parodiz 1982), some of whose findings are critically analysed herein. It is concluded that there is some evidence for correlation between these deposits and the Pebasian, but it is now based on sounder grounds, and ones almost entirely different from those they suggested.

The advances made in the present study have depended on the recognition that in the Magdalena Valley there are strong faunal links between the Santa Teresa Formation (Anderson 1928, San Juan de Rio Seco), originally dated as Eocene, and the La Cira Formation (Pilsbry & Olsson 1935) originally dated as Upper Oligocene or Lower Miocene. The fauna of the latter is shown to include the most common of the two species occurring in the underlying Mugrosa Formation, originally dated as Middle Oligocene. The first two are now thought to be Miocene, and the Mugrosa Formation cannot be separated from them on palaeontological grounds. The only argument in favour of the Mugrosa being pre-Miocene is that it lies between 780 and 2070 m below the La Cira fossil horizon, but this is far from conclusive. The newly-described La Tagua molluscan fauna has provided an important link between these Magdalena Valley faunas and those of the Pebasian. In addition, the La Taguan and Pebasian ostracod fauna (Sheppard & Bate 1980) has yielded confirmatory evidence that the two are of broadly similar ages.

Below are listed the rather limited number of taxa whose known distribution in the fauna of more than one region is considered to be of correlative value.

Taxa of value in correlation between regions

Pachydon. Described from the Pebasian, where it is the dominant faunal element. Now recognized in La Cira and Santa Teresa Formations of Magdalena Valley and abundant at La Tagua.

Pachydon cebada (Anderson). Common to La Cira and Santa Teresa Formations.

Pachydon hettneri (Anderson). Common to Santa Teresa and La Tagua faunas.

Pachydon erectus Conrad. Described from Pebasian, and present at La Tagua.

Mytilopsis. Found in La Cira, La Tagua and Pebasian faunas.

Mytilopsis scripta (Conrad). As above.

Liris. Described from Pebasian, otherwise known only from Tumbatú Formation of Chota Basin, Ecuador, by an unnamed species not occurring in the Pebasian.

Dyris tricarinata (Boettger). Described from and common in Pebasian. Also occurs at La Tagua and in San Cayetano of Loja Basin, Ecuador.

Longiverena eucosmia (Pilsbry & Olsson). Described, with several synonyms, from Mugrosa Formation and now also recognized in La Cira Formation, both of Magdalena Valley. Also from the basal Azogues and Loyola Formations of the Cuenca Basin, Ecuador and the Pebasian of Iquitos, Peru.

Sheppardiconcha lataguensis sp. nov. Very similar to *S. eucosmia*. Known only from La Tagua.

The age determination of non-marine strata is always a problem unless they either contain fossils, such as spores, which may also be found in the marine succession, or can be dated radiometrically. Palynological work in Ecuador has been discussed briefly by Bristow & Parodiz (1982), who found its conclusions too controversial to be satisfactory. Similar work in Colombia is reviewed on p. 333 (Magdalena Valley faunas), and seems, in contrast, to be basically sound, though in need of reinterpretation because of later changes in the position of the Oligo-Miocene boundary. Some doubt about the use of the palynological evidence must remain for two reasons. First, insufficient details about the geographical and stratigraphical location of the spore samples are available for their relationship with the molluscan localities to be understood. Secondly, it is suspected that some of the palynological samples were dated by reference to ages originally applied to the vertebrate and non-marine molluscan faunas rather than by reference to planktonic foraminiferal zones.

The palaeontological evidence for dating the deposits dealt with herein are listed below.

Age-diagnostic taxa

Mytilopsis scripta (Conrad). In addition to its distribution as given above, this species is now recognized in late Oligocene strata in the Pacific coastal strip of western Peru. It was originally described from there as *M. trigalensis* by Olsson (1931).

Mytilopsis sallei (Recluz). A widespread living Caribbean species, now recognized in the Pebasian and also in the late Oligocene of western Panama, as *M. dalli* (Clerc *in* Joukowsky, 1906).

Neritina ortoni Conrad. Confined to the Pebasian but also probably occurring in the Miocene (N8) Cantaure Formation of Venezuela, represented by a single specimen identified by Jung (1965) as *N.* aff. *woodwardi* Guppy.

Hemisinus brasiliensis (Moricand). *Hemisinus sulcatus* Conrad, described from the Pebasian, is assigned to this species now living in the Atlantic drainage of South America.

Hemisinus kochi (Bernardi). *Hemisinus sulcatus* de Greve, *non* Conrad, from the Pebasian of Iquitos appears identical to this living species, with a distribution similar to that of *H. brasiliensis*.

Verena crenocarina (Moricand). *Purpura woodwardi* Roxo from the Pebasian of Três Unidos is definitely a *Verena*, and appears to belong to this species, with a similar present-day distribution to the two species of *Hemisinus* above.

Necronectes proavitus (Rathbun). This crab was originally described from the Gatun Formation (probably mainly Upper Miocene) of Panama, and has been identified from the Loyola Formation of the Cuenca Basin, Ecuador (Collins & Morris 1976, Bristow & Parodiz 1982).

Pelocypris zilchi (Triebel). This ostracod, recorded by Sheppard & Bate (1980) from La Tagua, was the only member of the fauna they described known from outside the Upper Amazon Basin. It was described from strata in San Salvador of supposed Plio-Pleistocene age.

Vetustocytheridea bristowi (van den Bold). This ostracod species is described from the Loyola and Mangán Formations of the Cuenca Basin. Bristow & Parodiz (1982) regarded it as probably diagnostic of the Miocene. The genus is known only from the Miocene of the Caribbean and southern United States (van den Bold 1976).

Other evidence of age

The andesite underlying the Loyola Formation of the Cuenca Basin, Ecuador and radiometrically dated as 19–20 million years (Late Aquitanian, N5) (Snelling, unpublished report *in* Bristow & Parodiz, 1982: 8), effectively provides a maximum possible age for the Cuenca Basin deposits.

The similarities between the La Cira and Santa Teresa faunas of the Magdalena Valley and those of La Tagua means that they must have been deposited before the mountain building period in which the Cordillera Oriental of Colombia was sufficiently raised to block any connection between the Magdalena Valley and the Upper Amazon Basin. This event was dated by Campbell & Bürgl (1965) as occurring at the end of the Miocene. In this work they outline (1965: 583–585) the history of the eastern Cordillera. The same sedimentary cycles during the late Tertiary may be traced across it from the Magdalena Valley on its western flank to the Llanos to the east of it, leading them to conclude that it was not subjected to strong diastrophism or uplift until the end of the Miocene, though there were some preliminary movements prior to the deposition of the Upper Miocene (Honda Series). Overlying deposits assigned to the Pliocene were virtually unfolded. Elsewhere in this summary they referred to a new sedimentary cycle starting in the Middle Miocene before the deposition of the Colorado Series, which is thought (Butler 1942) to be the equivalent of the La Cira Formation of the Middle Valley. Campbell & Bürgl do not explain their evidence for dating these various events, except for a footnote (1965: 583) referring to the difficulty in identifying the Oligo-Miocene contact in the Colombian non-marine province because of the reassignment of the Aquitanian to the Miocene. On the basis of this currently accepted interpretation of the base of the Miocene, Hopping's work on the palynology (1967), summarized on pp. 333–334 (Magdalena Valley), placed the La Cira Formation (*sensu lato*) somewhere between the Oligo-Miocene boundary and Zone N10 of the Middle Miocene. Thus, Campbell & Bürgl and Hopping are more or less in agreement on a revised age for the La Cira Formation. In his later study (1970) on the Oriente of Ecuador, Campbell was still of the opinion that the link between that region and the Magdalena Valley, through a portal in the Mocoa region, was not closed until the late Miocene.

All the evidence so far presented points to the bulk of these faunas from both Colombia and Ecuador being of approximately the same age, probably Miocene. They clearly predate the late Tertiary Andean orogeny, and the main proviso must be about the accuracy with which this is dated in reference to the marine succession.

The Mugrosa Fauna from the Magdalena Valley, on stratigraphical but not on palaeontological grounds, might be distinctly older than the overlying La Cira Formation and therefore possibly pre-Miocene.

The Los Corros Fauna of the Esmeraldas Formation is, as discussed in the section on the Magdalena Valley faunas (p. 336), definitely older, being Oligocene or even possibly late Eocene.

The Pebasian faunas of the Upper Amazon Basin have in recent years been generally accepted as Pliocene, but on no firm palaeontological evidence. In fact, virtually all the evidence presented in this paper is entirely new. Living species are recognized in the Pebasian for the first time. These are *Mytilopsis sallei* (Recluz), *Hemisinus brasiliensis* (Moricand), *H. kochi* (Bernardi) and *Verena crenocarina* (Moricand). In contrast, no living species have been found in any of the other faunas discussed above, which are now regarded as Miocene. Again for the first time, fossil species occurring in other faunas are recognized in the Pebasian. *Pachydon erectus* Conrad and *Dyris tricarinata* (Boettger) are found both in the Pebasian and at La Tagua. The latter also occurs in the intermontane basins of Ecuador. *Longiverena eucosmia* (Pilsbry & Olsson) is common to the Mugrosa, La Cira, Loyola and basal Azogues Formations and also the Pebasian of Iquitos. The ostracod fauna described by Sheppard & Bate (1980) is discussed in the sections on the Pichana (Pebasian), p. 326, and the La Tagua, p. 173, faunas. The large proportion of species in common, particularly in view of the fact that they are thought to have lived in rather different salinities, suggests that these two deposits are of quite similar ages.

The Pebasian molluscan fauna differs very markedly from the living fauna, both in the presence of many extinct genera, and in that it contains taxa which, like those of the other faunas under consideration, indicate conditions of deposition very unlike those of the present day. Such changes, however, do not necessarily indicate the passage of a great deal of time, as witness the varied sequence of faunas during the Pleistocene in different parts of the world. If we accept Kätzer's (1903) hypothesis that an inland basin of deposition, roughly coinciding with the present-day Upper Amazon Basin, existed during the Tertiary until the drainage divide between it and the eastern end of the present Amazon was breached, then the Pebasian fauna, along with the Colombian and Ecuadorian faunas, lived before the breakdown of the drainage divide. This event would have radically altered conditions in that basin and allowed the entry of the present-day eastern Amazonian fauna.

The balance of the evidence suggests that a Pliocene age for the Pebasian cannot be entirely ruled out. However, a Miocene age, broadly similar to that of the other faunas, seems much more probable. The few living species present in the Pebasian but absent in the other faunas might indicate that the Pebasian was possibly the youngest of this group.

It is clear from Simpson (1961) and from examination of faunal lists that there are several other faunas, from localities lying to the south of the true Pebasian outcrop and situated mainly in the Rio Jurua area, which are distinct from those of the Pebasian. The molluscs listed from these localities appear to be approximately the same as those in the present-day Amazonian fauna, and therefore have virtually nothing in common with that of the Pebasian. Certainly, none of the living species now recognized in the Pebasian has been recorded in any of these faunas: they also lack all the extinct genera characteristic of the Pebasian. The molluscan evidence is that these faunas are indisputably younger than the Pebasian. Their age cannot be deduced from the data available, but their similarity to the living fauna suggests that they might be Pleistocene or even Holocene. There seems to be no reason to suppose that the mammal faunas of these localities are Pebasian.

Palaeogeography

At a very early stage in this study, the question arose as to the origin of the brackish to marine elements – mainly *Neritina*, *Mytilopsis* of the Dreissenacea and various genera, in particular *Pachydon*, of the Corbulidae – in the Pebasian and La Taguan molluscan faunas. Even before consulting any literature (Weeks 1948) on palaeogeography, it seemed apparent from consideration of the physical geography of the Continent that there were basically four possible connections between the upper Amazon region and the sea: northwards to the Caribbean; eastwards along the course of the present-day Amazon, between the Guyana and Brazilian shields; southwards towards the estuary of Rio La Plata; or westwards to the Pacific.

At first sight, the Caribbean connection appeared to be the most attractive option, bearing in mind that the Pebasian faunas were generally considered to be Pliocene, by which time the Andes would have reached some considerable height and effectively blocked a westward connection to the Pacific. Growing familiarity with both the literature and additional relevant fossil faunas, which were clearly pre-Pliocene, suggested that the westward connection was also a distinct possibility. However, none of the evidence for either of these two alternative routes seems to exclude the other. On the other hand, with respect to the remaining alternatives, no good evidence has been found suggesting that migration took place of either marine or brackish taxa up the present Amazon Valley from the Atlantic, or northwards from La Plata. Nevertheless, similarities between the fossil freshwater faunas, in particular those genera of Hydrobiidae now placed in the Lithoglyphinae, of the Upper Amazon Basin and the Recent Amazonian and La Plata faunas suggest that possible fresh-water links between these regions are worthy of consideration. Gardner (1927) suggested such a link, based on her assumption that *Azara (= Erodona)* and *Anisothyris (=Pachydon)* were closely related: this, however, is not the case as the two have very different hinges (Fig. 355, p. 289).

Sheppard & Bate (1980: 121), on the basis of their study of the ostracod faunas of La Tagua and Pichana, which they considered to be contemporaneous and Plio-Pleistocene, suggested that the sea lay to the east and that a marine transgression had entered along the line of the present Amazon Basin (? or valley). Their palaeogeographic map (1980: 120, text-fig. 5) was constructed to explain the salinity gradient between Loc. 54, La Tagua (where the only ostracod was a fresh-water species), the nearby Loc. 33/480–560, La Tagua, with a mixture of fresh-water, brackish and marine ostracod species, and Pichana, some 500 km further south, with a greater proportion of brackish and marine ostracods and only two fresh-water species. Their map, showing an east–west coastline lying to the south of Pichana, could equally well be interpreted as suggesting a connection with the Pacific: a possibility they had dismissed because of the Andes mountain chain. Furthermore, other explanations may be put forward to explain this salinity gradient. Thus, rotation of their map so that the coastline lay slightly to the east of Pichana in a north–south direction would lead to the inference that there was a channel in open sea, parallel to the coastline, running towards the Caribbean and La Plata. Other alternatives present themselves as the hypothetical coastline is rotated. For example, if it lay in a SE–NW line somewhere to the south-west of Pichana, the same salinity gradient could be drawn into the map, and a connection with the Marañón Portal again becomes a possibility. The salinity gradient can also be explained in the context of Late Cainozoic geography not being static, and the various deposits not being precisely contemporaneous. The two La Tagua ostracod faunas indicate different facies, and samples from the others, including different fossiliferous layers at Loc. 33, were not studied. It may therefore be suggested that though valuable ideas are presented about the facies and the relative ages of these deposits, the palaeogeographic evidence in favour of an eastward connection down the Amazon Valley is far from conclusive.

The Pebasian Basin, eventually isolated from the sea, and with internal drainage, is in some respects analogous with the Sarmatian Basin of the eastern European Miocene. Here, a small number of originally fully marine molluscan taxa, including *Dorsanum* of the Nassariidae and various Cardiidae, developed wide morphological variation in response to falling salinity caused by influx of fresh water from rivers draining into the basin. Such basins are characterized by faunas with comparatively few species showing wide variation and by a lack of exclusively marine groups such as corals, bryozoans and echinoderms. On the other hand, some of these, as well as brachiopods and cephalopods, are present in the diverse fauna of the shrinking Permian Zechstein Sea of northwestern Europe, bordered by arid deserts and with rising salinity. Contrasting with the Zechstein, Runnegar & Newell (1971) recognized in the Permian of southern Brazil a relict fauna, which they compared with that of the present-day Caspian Sea and which lacked these typical marine elements.

Boltovsky (1958) suggested that the Caribbean had been the source of the fauna of the living fresh-water and low salinity foraminifera of the La Plata region. As they are absent from the Brazilian coast, he thought they had not reached the La Plata estuary by this route, but through the Continent. Among the various works he quoted in support of his ideas, he referred to Ihering (1927), whose Karte 1 postulated a connection between the Caribbean and Patagonia. Ihering's reconstruction, however, reflected his views of Upper Cretaceous palaeogeography, and his Eocene map (Karte 2) showed that this seaway had closed. It should be borne in mind, when reassessing relatively early palaeogeographic maps which were made without taking the theory of continental drift into account, that they were attempting to explain the distribution of faunas. Ihering's maps are therefore still of relevence in that he was postulating faunal separation of Patagonia and the Caribbean occurring near the beginning of the Tertiary. A further argument against Boltovsky's view is provided by the lack of foraminifera in the Pebasian, which would have straddled the route of his postulated migration. Although ostracods are well known from the Pebasian (Gardner 1927, Purper 1977, Sheppard & Bate 1980), no foraminifera have been found. None have been encountered by the present author, who provided Sheppard & Bate with the matrix yielding their fauna.

The discovery of the La Tagua faunas had immediately suggested a northward extension of the Upper Amazon, Pebasian, Basin, parallel to the still rising Andes, and it seems reasonable to postulate that to the east of the Andes chain, during the Tertiary, there lay a north–south trough up to 500 km wide, occupied by a continually shifting pattern of streams, swamps, and lakes of varying salinity and offering intermittent connections with the Caribbean. It would not seem to be necessary for the connection between the sea and the heart of the basin to be direct at any one time. A series of lakes continually splitting and merging with each other, or perhaps becoming reconnected by streams, would enable taxa to progress gradually from one area to another. Lake Titicaca, with its somewhat unusual, isolated, molluscan fauna (Haas 1955), presumably was once connected, in one of the ways suggested above, to other significantly large bodies of water in which the ancestors of its present faunas lived.

Few previous workers have supported the case for a Caribbean connection. Steinmann (1929: 207) devoted little more than a sentence to the proposition, whilst Oliveira & Leonardos (1943: 640) quoted Maury – without any reference to their actual source – as suggesting a link between the Pebasian Pliocene of the Upper Amazon and the Antilles. They may have been referring either to her views that this correlation was probable (Maury 1925*b*: 17–18) or to a later paper (Maury 1937: 12) in which she commented on Guppy's (1908) unillustrated work on the Comparo Road fauna of Trinidad. Guppy (1908: 114) had identified two Pebasian species, *Anodon batesi* Woodward and *Hemisinus sulcatus* Conrad, but it seems likely that these were misidentifications. Maury's own, more thorough, descriptions of Trinidad fossils (1925*b*) included descriptions of two new Comparo Road species, *Corbicula comparana* Maury, and *Hemisinus comparanus* Maury. Corbiculidae are not present in the Pebasian, whilst Maury's illustrations (1925*b*: pl. 46, figs 9, 10) of *Hemisinus comparanus* show it to differ markedly from any known Pebasian species. It is therefore concluded that there is no molluscan palaeontological evidence for this particular correlation, which Maury stated (1937: 12) had been accepted ever since in the Trinidad literature.

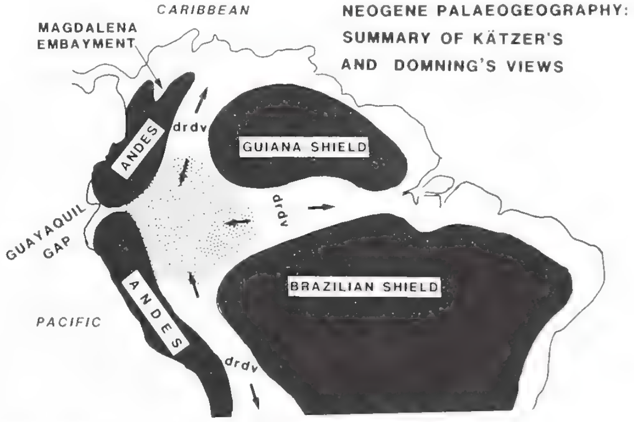


Fig. 453 Neogene palaeogeography, a summary of the views of Kätzer (1903) and of Domning (1984). Key; drdv, drainage divides; black arrows, direction of flow of rivers; stipple, inland brackish- to fresh-water sedimentary basin. The connection between the sedimentary basin and the Pacific Ocean through the Guayaquil Gap closed during the Neogene. In addition, the drainage divide in the present Amazon Valley was eliminated by headward erosion of rivers flowing eastwards as well as others flowing westwards; this resulted in the formation of the present-day Amazon system draining eastwards into the Atlantic Ocean after the closure of the connection with the Pacific. Note that the Magdalena Embayment is shown opening only northwards towards the Caribbean. Modified from Kätzer (1903) and Domning (1984) (compare Fig. 2, p. 170).

There has been more consistent support (Campbell 1970: 20; Domning 1982: 599, 607, 612, maps figs 8, 8a, 9; Fittkau 1974: 105–110, maps figs 10–13; Harrington 1962: 1801–1804, maps figs 27–30; Oliveira *in* Jenks 1956: 55) for Kätzer's (1903) hypothesis (Fig. 453) that there was a connection between the Pacific and the Amazon Basin through the so-called Marañón Portal, which was finally closed during the Miocene. Von Ihering (1927: 68–9) explained the presence of marine shells in the Pebas Beds (which he dated as Eocene) as being owing to the presence of an east–west 'Amazonsmeer' (Karte 2) bisecting the Continent. Grabert (1983), writing later when plate tectonics were generally accepted, referred to the Amazon – Bénoué Graben, stretching from the Pacific coast of South America, across the Atlantic Ocean and through west Africa from Mount Cameroon to Lake Chad.

Domning (1982: 612) gave a useful updated summary of Kätzer's views. Prior to the Miocene Andean orogeny, most of the western and central Amazon Basin drained into the Pacific and the Magdalena, Orinoco and La Plata Basins were separated by drainage divides. The only direct access to the western and central Amazon Basin was from the Pacific, and was eventually lost because of the mountain barriers formed during the Miocene orogeny. This connection is thought to have lain in the Peruvian–Ecuadorian border area, rather to the south of the Bay of Guayaquil. This created an initially brackish basin during the Miocene and Pliocene, with an internal drainage system. Headward erosion of streams eventually broke through the eastern divide which separated this basin from the eastern part of the Amazon Valley, thus initiating the present drainage system.

Domning's own palaeontological evidence does not necessarily support this view fully. He referred (1982: 600) to the presence of the manatee *Potamosiren magdalensis* Reinhart, 1951 in the La Venta fauna of the Miocene Honda Group in the Magdalena Basin of Colombia. He also referred to a probably Plio-Pleistocene specimen from the Jurua Valley (1982: 603–4), identified as cf. *Trichecus* sp., which resembled the modern west Indian rather than Amazonian species of manatee. Either of these could have reached their final destinations just as easily by migration from the Caribbean as through the Marañón Portal.

Campbell (1970: 20) referred to large lakes forming in the Oriente region of Ecuador during the Tertiary after the late Cretaceous Laramide uplift. He argued that there was some connection with the sea through the Marañón Portal because fossiliferous intercalations containing brackish-water faunas were locally present. However, it would seem equally likely that the presence of these faunas in the Oriente indicated some connection with either the Magdalena Basin of Colombia or with the Pebasian Basin, or with both. The main point in favour of the Pacific connection are the reports (Tschopp 1953: 2337–9) of foraminifera in the Tertiary of the Oriente. Foraminifera have not been reported from the Magdalena Valley, nor La Tagua, nor the Pebas Beds, so cannot have migrated from any of these.

Several factors now combine to suggest that there is not as yet any one clear-cut explanation of the history of the origin of the Pebasian Basin and its faunas. During the Tertiary, before the Panamanian land bridge between South and Central America came into being in Plio-Pleistocene times, there existed (Woodring 1965, 1966) a single marine province – termed the Tertiary Caribbean Province – stretching from the coastal strip of north-western Peru, through western Ecuador and Colombia to the Caribbean. Thus, it would be theoretically possible for a species to be distributed throughout this province and migrate into the Pebasian Basin by any route available to it, either from the Pacific or from the Caribbean. The molluscan and other palaeontological evidence is discussed below.

Mytilopsis, a member of the Dreissenacea, is tolerant of wide variation in salinity and may be found in habitats varying from fresh-water rivers to hypersaline, isolated stretches of water subject to reduction by evaporation. Some of its present-day distribution may be the result of introduction to new areas by man, but its fossil occurrences show that it has been capable of unaided migration across definitely marine water. The genus is known to occur in the European Eocene (p. 279) and its earliest western hemisphere occurrences are both probably in the late Oligocene. *M. trigalensis* Olsson, from western Peru, is here placed in the synonymy of the Pebasian species *M. scripta* (Conrad). This species is now also recognized as occurring at La Tagua and in the La Cira Formation of the Middle Magdalena Valley in Colombia. The second Oligocene species, *M. dalli* (Clerc *in* Joukowsky) was first described from the Pacific coastal side of Panama, and is here considered to be a synonym of the living Caribbean *M. sallei* (Recluz). This living species is now recorded (p. 283) from the Pebasian. The genus *Mytilopsis* is unknown from the Atlantic coastal belt of South America and therefore does not appear to have migrated to the Pebasian Basin either up the Amazon or northward from La Plata. At the present day, the most southerly Pacific coast records of the genus is from rivers in northern Ecuador (Olsson 1961, Keen 1971).

Thus, neither of these Oligocene records of *Mytilopsis*, from western Peru and Panama respectively, can be taken as supporting evidence of one possible migratory route into the Amazon Basin rather than another. It is hypothetically possible for the Peruvian *M. scripta* to have entered the basin *via* the Caribbean and for the Caribbean *M. sallei* to have entered from the Pacific coast. Furthermore, the spread of *Mytilopsis* within the basin itself cannot be monitored, because of both the paucity of records and inadequate knowledge of the stratigraphy. Although both species are quite variable, the specimens of *M. scripta* from La Tagua, lying on Rio Caqueta, and La Cira, in the Middle Magdalena Valley about 500 km to the north, are remarkably similar. This raises the possibility of migration southward from the Caribbean up the Magdalena Valley, rather than along a route to the east of the Cordillera Oriental. This by no means exhausts the possibilities: for instance, the faunas of the Oriente of Ecuador are barely known and, in consequence, the region seems not to have been seriously considered as part of a through route for faunal migration.

The recognition of the normally marine family Vitrinellidae in the Pebasian indicates nothing more than some undefined, and possibly distant, connection with the sea. At the present day, rather similar Vitrinellidae occur both in the Caribbean–western Atlantic and Pacific provinces, whilst the fossil record of the family is extremely sparse.

Neritina often has an intertidal distribution analogous to that of *Littorina* in temperate seas. Some *Neritina* species are fresh-water and have been found in mountain streams. At the present day, the genus occurs throughout the Caribbean (Warmke & Abbott 1961), and its range continues along the Atlantic coast to about 27° S in southern Brazil (Rios 1965). On the Pacific coast, it occurs from California southwards to northern Peru at about 5° S (Keen 1971). Records of the genus as fossils in deposits of the coastal strips surrounding South America are rare, probably largely because it was living in inshore habitats where its chances of fossilization were slim. It is apparently unknown in the Tertiary of the Buenos Aires region (Comacho 1966). On the basis of its known fossil and Recent distribution, the only route eliminated for its entrance into the Upper Amazon region is from the Rio de la Plata estuary. As explained on p. 183, *Neritina* *ortoni* Conrad of the Pebasian is not entirely typical of the genus. Its operculum, known only from one specimen, appears to be unusual and certain features of its ventral surface are reminiscent of the marine genera *Velates* (Eocene) and *Smaragdia* (Recent). Deductions made from the distribution of *Neritina* should therefore be viewed with some caution. Nevertheless, examination of all known fossil and living taxa suggests that the greatest resemblance to *N. ortoni* is shown by the single specimen from the Miocene of the Paraguana Peninsula of Venezuela, identified as *N.* aff. *woodwardi* Guppy by Jung (1965). Like *Mytilopsis*, this could have entered the Upper Amazon Basin from either the Caribbean or the Pacific. The only other fossil *Neritina* to be considered are those from the non-marine deposits of the Cuenca Basin, Ecuador. Unfortunately, they are too poorly preserved for worthwhile comparisons to be made with other species. However, enough of their characters can be seen to show that none are close to *N. ortoni*. No deductions can be made concerning their origins.

The Corbulidae are, in general, marine, though some species tolerate the reduced salinity encountered in, for example, estuarine areas. *Erodona*, whose hinge clearly shows it to be unrelated to *Pachydon*, lives in the Rio de la Plata estuary in such profusion that it sometimes forms shell banks. The presence of members of the Corbulidae in the Pebasian is a sure indication of connection with the sea at some stage in the evolution of the basin. All Corbulidae considered here are assigned to the Subfamily Pachydontinae, which is expanded to accommodate not only *Pachydon*, but also *Pebasia* and *Ostomya*, all three of which are extinct, as well as the living *Guianadesma*. *Pachydon* is one of the most important elements of typical Pebasian faunas, and until recently was thought to be endemic. Its recognition here in both the Magdalena Valley deposits and in the La Tagua Beds is crucial evidence for a connection between these three areas. *Pachydon hettneri* (Anderson), described from the Upper Magdalena Valley, occurs at La Tagua. This and other similarities between the faunas of these districts is taken as proof that the La Tagua Beds and the La Cira formation are contemporaneous and were laid down before the Andean orogeny destroyed the link between the Magdalena and Amazon Basins. The only record from the Cuenca Basin of *?Pachydon* sp. is based on a single not very informative mould misidentified as *Pachydon* cf. *iquitensis* (de Greve) by Parodiz *in* Bristow & Parodiz (1982), and here reidentified as *Corbicula cojitamboensis* Palmer, a common fossil species of the Cuenca Basin. The potentially valuable evidence of Rutsch (1952), who reported *Pachydon* in the Neogene of Venezuela, was unfortunately not backed by illustrations of the fossils. Rutsch had seen the material in an oil company's collections in Venezuela and had made his identification, presumably either with the aid of his memory or of notes, after his return to Switzerland and examining the fossils from Iquitos described by de Greve (1938) housed in PIMUZ.

None of the remaining molluscs provides evidence of a connection between the Upper Amazon Basin and the sea. Although they may well belong to families which have marine or brackish members, they themselves do not necessarily fall into those categories.

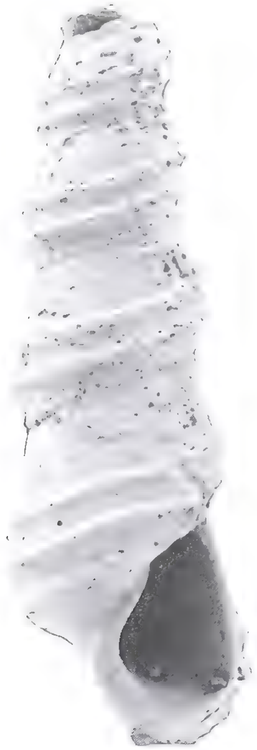
Both *Pebasia* gen. nov. (p. 315) and *Ostomya* are rare and endemic to the Pebasian. However, fossil species recognized here as belonging to *Guianadesma* have been wrongly assigned in the past to the clearly distinct *Ostomya*. All three of these genera are aberrant Corbulidae. *Pebasia* and *Pachydon* may well share common ancestry. *Ostomya* and *Guianadesma* may also share common ancestry but their connection with ordinary marine members of the family is obscure. *Guianadesma*, now living in rivers of the Guianas and tolerating brackish water, is now recognized fossil from the Neogene of Monogas State, northern Venezuela (Palmer 1945) and from rather poorly preserved material from the La Cira Formation of the Magdalena Valley (Pilsbry & Olsson, 1935). Its distribution suggests some link between these regions which does not necessarily involve areas to their south such as the Pebasian Basin and the Marañón Portal. The strength of this evidence, however, is undermined by the rarity of these genera and the poor preservation of the La Cira occurrence.

Some evidence for a fresh-water to possibly slightly brackish link with the Rio de la Plata estuary is provided by those members of the Hydrobiidae now assigned to the Lithoglyphinae, which is based on the living and Pleistocene European *Lithoglyphus*. The subfamily also occurs in North America. The Argentinian *Potamolithus* has also been assigned to it and may well be the closest living relative of endemic Pebasian genera such as *Eubora* and *Tropidobora*.

The Littoridininae are so ubiquitous that no conclusions can be drawn from their distribution pattern. Furthermore, their radiation in isolated areas such as Lake Titicaca suggests that they may be so subject to rapid morphological diversification that it becomes impossible to unravel their relationships. In contrast to the Littoridininae, the Cochliopinae are so poorly known in South America that their distribution pattern can hardly be used as a source of palaeogeographic evidence. *Nanivitrea*, described living on Cuba and Jamaica, is known from South America by a single Recent Venezuelan species and by *N. colombiana* sp. nov. (p. 213) from the La Tagua Beds.

The Unionacea and Mutelacea (swan mussels) and the river snails of the Thiaridae are nowadays distributed throughout the Amazon Valley as well as most of the other major river systems of the Continent, particularly those with Atlantic drainage. Tertiary fossil species, on the other hand, tend to be concentrated towards the west of the Continent, in the Pebasian, Cuenca and Magdalena Basins. This apparent change in distribution is of little significance beyond drawing attention to the fact that the main areas of non-marine deposition during the Tertiary lay in the north-western quadrant of the Continent.

The distribution of fossil molluscs provides not only evidence of connections between the Upper Amazon Basin and other regions, but also some indication of the extent of that basin. From earlier parts of this section, it has become apparent that there was a connection between the Pebasian Basin, the La Tagua Beds of the Rio Caqueta Valley and the deposits of the Middle and Upper Magdalena Valley. *Longiverena eucosmia* (Pilsbry & Olsson, 1935), described from the Middle Magdalena Valley, is now thought to occur at Iquitos in the Pebasian Basin and in the Cuenca Basin, whilst the rather similar *L. colombiana* sp. nov. occurs at La Tagua. *Pachydon* is known from all these deposits, though the Cuenca record is doubtful. Records of the genus from the Amazon Valley as far apart as Yurimaguas in the west and the Rio Inuya region of the upper Ucuyali Valley in the south (Willard 1966) give some indication that this basin extends well away from the classic Pebasian localities. An intriguing record of rocks 'crowded with *Tellina*' from Bolivia (M[illegible] 1922) could possibly be of *Pachydon* and might [illegible]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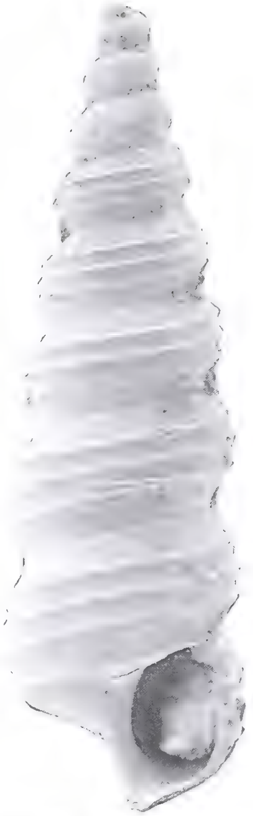
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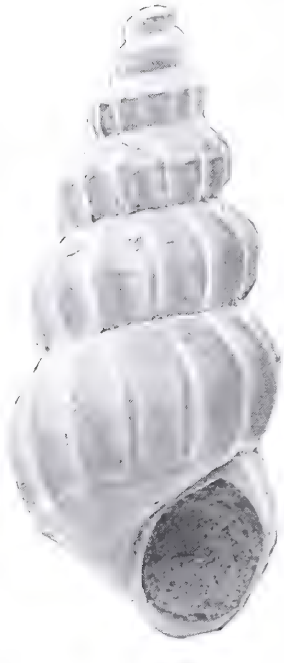
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Figs 454–455 *Dyris gracilis* Conrad. Pebasian; Canamá, Peru; Barrington Brown Colln. Front views, × 20. **454**, GG22416; **lectotype** (herein selected) of *Melania bicarinata* Etheridge (1879), originally figured by Etheridge (1879: pl. 7, fig. 7). **455**, GG22421; holotype of *Melania tricarinata* Etheridge (1879), originally figured by Etheridge (1879: pl. 7, fig. 6).

Fig. 456 *Liris scalarioides* (Etheridge). Pebasian; Canamá, Peru; Barrington Brown Colln. GG22419; **lectotype** (herein selected) of *Melania scalarioides* Etheridge (1879), originally figured by Etheridge (1879: pl. 7, fig. 8). Front view, × 20. (See also Fig. 139, p. 206).

southward extension of the basin towards Rio de la Plata, blocked further south by a drainage divide.

The eastern limit of the Pebasian Basin seems to be marked fairly closely by the long-known classic localities. So far, the most easterly Pebasian fossils known are those described from the neighbourhood of São Paulo da Olivença (Costa 1980). Brazilian geologists have mapped both the Pebasian deposits themselves and also apparently later beds stretching as far east as Manaus and encompassing deposits of the Rio Jurua as Solimões Formation. This problem is discussed in more detail in the section on Brazil. It is concluded, however, that they are not an extension of the Pebasian Basin and, where fossiliferous, contain different and younger faunas.

No Tertiary non-marine molluscan fossils have been named from the Oriente of Ecuador, though their presence was noted (Campbell 1970: 20, Tschopp 1953: 2338). The discussion on the Cuenca Basin deposits elsewhere in this work show that its molluscan faunas have far less in common with the Pebasian than formerly suggested (Bristow & Parodiz 1982). The presence of both *Liris* and *Longiverena eucosmia* suggest some connection. The Cuenca Basin is here regarded as part of the same general depositional area as the Pebasian. Differences in the fauna may be interpreted as signifying some difference in facies. It seems possible that the Ecuadorian Oriente provided links between many of the main faunas dealt with herein. It lies between the Cuenca and Pebasian basins, situated to its west and east respectively, and it also lies to the south of both the La Tagua region and the Magdalena Valley. Campbell (1970: 7) regarded it as the eastern margin of a much wider area of sedimentation before the last uplift of the Andes in the late Tertiary, pointing out that it thinned markedly to its east, where only a veneer of Tertiary sediments lay on basement rocks. He also wrote (1970: 8) that the Oriente had palaeogeographic connections with the Magdalena Basins, with a portal between the Central and Eastern Cordilleras of Colombia remaining open until the late Tertiary uplift. This portal probably lay (1970: 25) in the Mocoa area of the Putumayo district.

The palaeogeographic implications of manatee distribution (Domning 1982) has been discussed, p. 352. The occurrence of the crab *Necronectes proavitus* in the Cuenca basin (p. 349) is of particular interest. The species was described from the Gatun Formation (now probably best dated as late Miocene) of Panama. Moreover, *Necronectes* is an uncommon genus (S. F. Morris, BMPD, personal communication). The implication of this is that some connection between the Cuenca Basin and the sea existed and that the source of the *Necronectes* was the Neogene Caribbean Province, which extended down the Pacific Coast (Woodring 1966). Here again, this occurrence cannot be taken as positive proof of one migration route rather than another: the Pacific coast is, however, much closer than the Caribbean to the Cuenca Basin.

To conclude: as suggested above, p. 350, the evidence is that a connection between the Upper Amazon Basin and the sea was necessary in order to explain the character of its molluscan fauna. Sheppard & Bate (1980) provided confirmation of this by describing some ostracods, which they consider to be definitely marine. On balance, it appears that there may have been more than one such connection. One may have been through the Marañón Portal to the Pacific in the

Peruvian–Ecuadorian border region; the second would have been with the Caribbean, either through the Magdalena Valley, or further east, through areas from which such fossil faunas are completely unknown. A non-marine connection northwards towards the northern part of the Continent would help explain the distribution of some freshwater molluscs. In addition, other non-marine connections with the Lower Amazon Valley and with the Rio de la Plata region of Argentina are distinct possibilities.

Palaeoecological summary

As far as is known, the bulk of the material examined was not collected bed-by-bed with palaeoecological studies in mind. It must therefore be taken into account that the total fauna reported from any particular locality probably came from several different horizons. The faunas of more than one locality were sometimes combined by early collectors, such as Hauxwell and Steere, whose fossils were described in works by Conrad (1871*b*, 1874*a*) and Woodward (1871). Hartt (1872) quoted Steere's remarks that some bed was richer in bivalves than gastropods, or vice-versa. Brown (1879: 80) gave some details of specific associations that he had observed at Canamá, but sadly his efforts were largely nullified by the loss of many of his fossils, described in Etheridge (1879), with the result that it is not always possible to update their joint determinations. In some instances, the most reliable guides to co-occurrences and relative abundances of species are provided by the few hand specimens of sediment containing a selection of fossil specimens. Such samples may also show whether it was a life or death assemblage, for instance by the occurrence of bivalves with both valves together. More accurate details of specific associations are provided for some, but by no means all, localities in Pilsbry & Olsson (1935) for Magdalena Valley faunas, and in de Greve (1938) for the collection made by Peyer from Iquitos. Examples of modern, well documented collections are those of Bristow from the intermontane basins of Ecuador (Bristow & Parodiz 1982) and the CAE collections from La Tagua, made by Eden and his associates.

De Greve (1938: 117) lists the views on facies of all authors prior to that date who dealt with Pebasian faunas: these range from fresh-water through to marine. Wrong determinations have coloured such opinions, and even as late as 1970, von Buerlen (p. 334) referred to the presence of *Corbula, Tellina, Cerithium, Mesalia* and *Natica*, which he grouped as marine genera, occuring along with fresh-water *Anisothyris, Unio, Hydrobia, Melania* and others. The records of *Corbula, Tellina* and *Anisothyris* can all be referred to *Pachydon*, whilst *Dyris ortoni* was originally assigned to *Mesalia* by Gabb (1869). The fresh-water *Sheppardiconcha coronatum* was first described under *Cerithium* by Etheridge (1879). This species was described by Gardner (1927: 308) as a member of the *Potamides* group, which she stated is not known to penetrate the upper courses of rivers. The record of *Natica* can only have been based on the erroneous interpretation of a shell boring by Woodward (1871: 102) in a specimen now the holotype of *Eubora woodwardi* Kadolsky (p. 216). *Purpura woodwardi* Roxo (1924) from Três Unidos, belonging to a muricacean genus and not listed by von Buerlen (1970), was first recognized as belonging to *Verena* of the Hemisininae by Santos & Castro (1967). This change is recognized on p. 253: it is now suggested that Roxo's species is synonymous with *V. crenocarina* (Moricand), the type species of the genus and now living in the rivers of eastern Brazil.

Table 2 Habitat preferences of constituents of fossil faunas.

	L/E	if A	r	mm	br	fw	land
Neritina	L	–	C	*	*	*	–
Littoridininae	L	–	VC	*	*	*	–
Dyris, Liris	E	–	VC	–	(*)	(*)	–
Littoridina (s.str.)	L	A	–	–	?*	*	–
Heleobia	L	A	–	*	*	*	–
Cochliopinae	L	–	R	–	*	*	–
Nanivitrea	L	–	R	–	–	*	–
Lithoglyphinae	L	–	FC	–	–	*	–
Potamolithus	L	A	–	–	–	*	–
Eubora, Tropidobora	E	–	C	–	–	(*)	–
Toxosoma	E	–	C	–	–	(*)	–
Vitrinella	L	–	R	*	(*)	–	–
Hemisininae	L	–	FC	–	–	*	–
Sheppardiconcha	E	–	C	–	–	*	–
Basistoma	L	A	–	–	–	*	–
Hemisinus	L	–	R	–	–	*	–
Longiverena	L	–	FC	–	–	*	–
Verena	L	–	R	–	–	*	–
Aylacostoma	L	–	R	–	–	*	–
Hebetancylus	L	–	VR	–	–	*	–
Orthalicus	L	–	VR	–	–	–	*
Unionacea, Mutelacea	L	–	R	–	–	*	–
Mytilopsis	L	–	R	–	–	*	–
Corbulidae	L	–	VC	*	*	–	–
Corbula	L	A	–	*	*	–	–
Pachydon	E	–	VC	–	(*)	(*)	–
Pebasia	E	–	VR	–	(*)	(*)	–
Ostomya	E	–	VR	–	(*)	(*)	–
Guianadesma	L	–	VR	–	(*)	(*)	–

Key to Table:

Column 1,	Living or Extinct
Column 2,	A, if absent in fossil faunas (i.e., genera included for comparative purposes only)
Column 3,	r, rarity: VC, very common; C, common; FC, fairly common; R, rare
Columns 4–7	mm, marginal marine; br, brackish water; fw, fresh water; land. Asterisks denote known distribution of living taxa; asterisks in brackets, the inferred distribution of extinct taxa.

Most of the systematic changes reported above are at superfamilial or familial level. Their net result is the elimination of marine taxa in favour of those living predominantly in a non-marine environment. In addition, not only the Corbulidae but also *Neritina*, *Vitrinella*, and *Mytilopsis* are indicative of some past or present connection with the sea, with the attendant possibility of brackish conditions. Such taxa are of the utmost importance when considering the wider palaeogeographic implications: they are, however, not sarily reliable guides when dealing with narrower problems such as the assessment of salinity at a particular locality.

Genera of Corbulidae, such as the widespread *Pachydon*, would have evolved from a marine, possibly inshore or even estuarine, ancestor. *Pachydon* possibly lived in a very similar environment to that of the present-day *Guianadesma*, found both in and above the tidal reaches of rivers in the Guianas. The Neritacea are predominantly marine, but include the fresh-water *Theodoxus*. *Neritina* itself is primarily a tropical intertidal genus; at the present day, several Central and South American and Caribbean species have invaded streams, and live in fresh water well away from the tidal zone. None, however, have been found at any considerable distance from the sea. *Mytilopsis* has a very wide salinity tolerance, but, like *Neritina*, and in common with other Dreissenacea, it appears to be absent from stretches of fresh water well away from the sea. The sea would appear to be a necessary part of any route whereby these two genera can establish a bridgehead when colonizing an entirely new area, such as the Tertiary inland basin of north-western South America.

Many of the localities under consideration have yielded faunas giving apparently contradictory evidence of facies, because their constituent species indicate a mixture of different environments. In some cases, this may well be the result of amalgamation of the faunas from different beds within the section, as discussed above. The proportions of the fauna indicating particular environments is always of importance: it would be reasonable to give more weight normally to evidence provided by the more common taxa, rather than to that to be deduced from the presence of rarities or of species only represented by possibly transported broken fragments. When two species occur with fairly similar frequencies, preference should clearly be given to the facies evidence provided by that species indicating a restricted environment rather than by a more tolerant species. Such criteria must be borne in mind when assessing the probable environment of extinct taxa. These points may be illustrated by the distribution of *Mytilopsis*, in particular with reference to its occurrence alongside fresh-water snails of the family Thiaridae, in different faunas.

An example of fresh-water occurrence of *Mytilopsis* is at the Rio Oponcito locality of the La Cira Formation of the Magdalena Valley. The fauna consists of *Mytilopsis* and *Guianadesma*, both of which can exist in a wide range of salinities, occurring with *Verena* and all four of the species of Unionacea and Mutelacea known from this Formation: all of these other taxa are exclusively fresh-water. *Pachydon*, which is present elsewhere in the La Cira Formation, is absent. (Determinations given by Pilsbry & Olsson (1935: 19), revised.)

In the Pebasian of Pichana, on the other hand, *Mytilopsis* is rare. The fauna is dominated by *Pachydon*, with *Neritina*, *Dyris* and *Liris* also important. None of the other genera present, mainly extinct Lithoglyphinae, are particularly common. Exclusively fresh-water taxa are rare. The Thiaridae and Mutelacea are represented only by the holotypes of *Hemisinus sulcatus* Conrad (*H. brasiliensis* herein, p. 244) and *Anodon batesi* Woodward (*Anodontites* herein), and the only Unionacea found are three juvenile *Diplodon*. Most of the ostracods are indicative of either brackish or marine conditions (Sheppard & Bate 1980), confirming the evidence suggested by the molluscan fauna, in which genera with known or probable wide salinity tolerance, such as *Pachydon*, *Neritina* and *Mytilopsis*, occur in a fauna almost totally lacking in fresh-water elements.

The Pebasian fauna of Iquitos, which includes *Mytilopsis*, is similar in most respects to that of Pichana except that fresh-water Thiaridae are important. *Sheppardiconcha tuberculifera* (Conrad) is reported as being represented by over 250 shells (Conrad 1874*b*, Pilsbry 1944). *S. coronata* (Etheridge), *Longiverena eucosmia* (Pilsbury & Olsson) and *Hemisinus kochi* (Bernardi) also occur (de Greve 1938). It may be suspected that the salinity here was less than at Pichana. Other Pebasian localities in which *Mytilopsis* occurs with abundant Thiaridae are Canamá, Três Unidos, and Puerto Nariño.

It thus appears that *Mytilopsis* occurs in sediments laid down in water of varying salinity: this reflects its present-day wide salinity tolerance. This, in turn, suggests that several of the extinct genera were also tolerant of a range of salinity. Of these, the most important is *Pachydon*, which occurs in many faunas, including all those used above to illustrate the example afforded by *Mytilopsis*. In fact, it might well be that different species of *Pachydon* – and perhaps this applies also to other genera – are indicative of particular salinities: however, I have not pursued this point. The remaining genera in these faunas are dealt with adequately in the palaeogeography section, above. Many occur at several fossil localities indicating a range of salinities, nearly all of which were probably rather low.

Finally, might not ostracods possibly change their facies

Table 3 Breakdown of elements of north-western South American fossil faunas by habitat and known distribution.

(1) Living marginal marine genera indicating links with sea.	*Neritina* *Mytilopsis* *Vitrinella*
(2) Typical modern South American fresh-water genera, with Recent distribution mainly on eastern side of continent.	*Hemisinus* *Verena* *Longiverena* *Aylacostoma* *Hebetancylus* *Diplodon* *Anodontites*
(3) Living in both brackish and fresh water in the Guianas.	*Guianadesma*
(4) Otherwise only known as living mainly in the Caribbean region except for one South American species (from Venezuela). Fresh-water, but with brackish-water relatives.	*Nanivitrea*
(5) Extinct genera first described from and endemic to Pebasian.	*Eubora* *Tropidobora* *Toxosoma* *Pebasia* *Ostomya*
(6) Extinct genera first described from Pebasian and since recognized in other South American fossil faunas.	*Dyris* *Liris* *Pachydon*
(7) Extinct genera first described from Cuenca Basin and since recognized in other South American fossil faunas.	*Sheppardiconcha* *Ecuadorea* (subgenus of *Diplodon*)

preferences in a manner analogous to *Pachydon*? This genus, with presumed marine ancestry, has evolved and proliferated in brackish- to fresh-water environments in the Tertiary Upper Amazon Basin. Ostracods are generally accepted as excellent facies indicators, but in this basin their facies may be a matter of inference to a greater extent than usual. All but one of the species described from Pichana and La Tagua by Sheppard & Bate (1980) are new, and one of the supposedly marine genera, which is known from both localities, is also new.

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APPENDIX: GUIDES TO LOCALITIES

Entries marked * are dealt with in more detail in separate individual sections, at the pages indicated.

A. Peru

Aguaytia river valley. 110 km S of Contamana, 25 km W of Ucuyali valley. Bassler collected (as *Anisothyris*) *Pachydon erectus* Conrad, *P. carinatus* Conrad, *P. obliquus* Gabb and (as *Liris*) *Dyris tuberculata* (de Greve); det. Willard (1966: 69).

Ambayacú, Rio. 3° 19′ S, 71° 51′ W. Flows south into R. Marañón. Pebas and Old Pebas are near the mouth of this river.

Ampiyacú, Rio. Alternative spelling of above.

Barreiras Braga. Not in gazetteer. On Rio Javari, downstream from Canamá. Brown (1879: 78) reported shells similar to those of Canamá.

Cachiyacú, Quebrada. 7° 22′ S, 74° 52′ W. Tributary joining R. Ucuyali just S of Contamana. Good exposures of Ucuyali Formation (Kummel 1948: 1260).

Canamá (* p. 327).

Cocani, or **Coccani**, Quebrada. 10° 32′ S, 73° 58′ W. Lower part of Rio Inuya valley. Bassler collected in 1922 fossils identified (Willard 1966: 69) as *Anisothyris* sp. and *Calyptraea* sp. (The latter could, however, be a misidentification of *Tropidobora*.)

Cochaquinas (* under Pichana, p. 324).

Contamana. 7° 21′ S, 75° 03′ W. Ucayali Formation (Kummel 1948: pl. 1).

Contamana Group. Fossils collected by Singewald (1928) and described by Pilsbry (1944) from **Pachitea River** section (q.v.). Kummel (1948: 1259–60) stated that the folded Contamana Group, of probable Eocene to Miocene age, was overlain by flat-lying Pliocene beds, which he inferred might be the same as the Pebas Beds of the Amazon Valley between Iquitos and Tabatinga. He mentioned no fossils from these overlying beds, however, and later went on to discuss the **Ucayali Formation** (q.v.).

Cushabatay, Rio. Flows eastwards to join R. Ucayali N of Contamana. Good exposures of **Ucayali formation** (Kummel 1948: 1260).

Filipe del Acquia. 10 km upstream from Iquitos on Rio Marañón. Bassler collected in 1928 *Corbula* sp. (?=*Pachydon*), *Anisothyris* (=*Pachydon*) *obliqua* (Gabb), *A. carinata* Conrad, *A. hauxwelli* Woodward (=*A. tenua* Gabb), *Lunatia* sp. (?=*Eubora*), *Turbonilla* (=*Liris*) *minuscula* (Gabb), *Isaea* (=*Dyris*) *ortoni* Gabb; ident. Willard (1966: 65–6).

Inuya, Rio. 10° 41′ S, 73° 30′ W (see **Cocani**).

Iquitos. 3° 42′ S, 73° 42′ W (* p. 331; see also **Filipe del Acquia**).

Iquitos Formation. Rivera (1956: 49) referred to Iquitos Formación of Steinmann (1930: 213; not seen by me). In the first, German, edition of this work (1929: 206), Steinmann referred merely to the Neogene of Iquitos without erecting a Formation.

Machira Creek. Good exposures of **Ucayali Formation** (q.v.) 5 km S of Cachiyacú (7° 22′ S, 74° 57′ W), near Contamana (Kummel 1948: 1258, 1260).

Manseriche (see **Pongo de Manseriche**).

Mazan, Rio. Near confluence of Rio Mazan and Rio Napo (3° 28′ S, 73° 11′ W), 30 km N of Iquitos, Bassler collected in 1924 *Pachydon carinatus*, *P. amazonensis*, *P. obliquus*, *P. erectus*, *Neritina ortoni*, *N. etheridgei*, *Pseudolacuna macroptera*, *Hydrobia confusa* and *Liris minuscula*. (Willard 1966: 68). This fauna is Pebasian.

Negro Urca. On Rio Negro, 200 km NW of Iquitos (3° 05′ S, 72° 40′ W). Bassler collected in 1926: Serpulae (?), *Lingula, Triplodon latouri* (Pilsbry & Olsson 1935), *Pachydon cuneatus, P. obliquus, P. erectus, P. amazonensis, Neritina amazonensis, Eubora crassilabris, Hydrobia* sp. (internal casts only, ?= *Dyris*), *Longiverena tuberculifera*. (Willard 1966: 66). The fauna is Pebasian. The record of *Lingula* is surprising and has not been checked by me. It might be a fresh-water limpet of the Ferrisiidae.

Omaguas. 4° 08′ S, 73° 15′ W. Fossils reported by natives (Conrad 1871*b*: 192).

Pachitea, Rio. Section in Red Beds, now **Contamana Group** (q.v.). Singewald's collection (1928: 463) was identified by Pilsbry, and eventually described by him (1944). Apparently (Singewald 1928: 457) near Quebrada Pumayacú (9° 10′ S, 74° 40′ W). Also mentioned in Kummel (1948: 1259).

Paucarparta. On Rio Marañón (4° 13′ S, 73° 18′ W). Singewald collected species of *Diplodon*, described by Marshall (1928*a*) as *Prodiplodon singewaldi* and *P. paucarpartensis*. Assumed to be Pebasian.

Pebas. 3° 20′ S, 71° 49′ W (* p. 322; see also **Pichana**).

Pebas beds, Pebas clays. Terms used by Hartt (1872: 54).

Pebas Formation. Term introduced by Costa (1980: 635). The term Pebasian is used informally in this paper for Pebasian Fauna, Pebasian Age and Pebasian Basin. See discussion in Introduction, p. 169.

Pichana (* p. 324). Near **Cochaquinas** (q.v.), on S side (= right bank) of Rio Marañón (3° 31′ S, 71° 43′ W).

Pichua. Alternative, incorrect spelling of **Pichana**.

Pongo de Manseriche. 4° 20′ S, 77° 15′ W. (Pongo = canyon or gorge). Just below confluence of Rio Santiago and Rio Marañón, about 800 km above Iquitos. Singewald (1927: 491) referred to poorly preserved fossils, possibly similar to those from the Red Beds of Rio **Pachitea** (q.v.). Singewald also noted, outside the pongo, grey shale which included lignitic coal and brackish-water (un-named) Pliocene fossils, which he equated with those of Pebas.

Old Pebas (* under **Pichana**, p. 324). On left (north) bank of Rio Marañón, about 2 miles (*c.* 3 km) below mouth of Rio Ampiyacú.

Red Beds (see **Pachitea**).

Rumi Tuni. (2° 05′ S, 74° 27′ W). Valley of Rio Napo, 225 km N of Iquitos. Bassler (? 1925) collected *Pachydon amazonensis, P. obliquus, P. carinatus, P. erectus, Congeria?* (= *Mytilopsis*), nacreous bivalve fragments (? naiades) in coquina, *Neritina etheridgei, Hydrobia confusa, Longiverena tuberculifera* and *'Ampullina (Mesalina) ortoni* (Gabb)' (?= *Dyris ortoni*). Other collections from the neighbourhood yielded similar faunas and also *Arca* (?), *Triplodon latouri* (Pilsbry & Olsson), *Aperistoma* and *Eubora crassilabra*; det. Willard (1966: 66–68). Most of these species are typical of the Pebasian: the exceptions may well be misidentifications.

Santa Isabel (see **Yurimaguas**).

Sarayaquilla/Saroyaquilla, Rio. Flows eastwards to join Rio Ucayali (7° 00′ S, 75° 10′ W). Excellent exposures of Ucayali Formation (Kummel 1948: 1260).

Três Unidos (*p. 329). On Peruvian bank of Rio Javari, 4° 24′ S, 71° 13′ W.

Ucuyali Formation (Pliocene to Recent). About 30 m of horizontal clays etc., lying discordantly on Contamana Group in region of rivers Ucayali, Sarayaquilla and Cushabatay. Unnamed plant, fresh-water bivalve and gastropod fossils reported (Kummel 1946: 134; 1948: 1260). Fauna is possibly Pebasian (see **Aguaytia, Cocani** and **Ucayali Valley**).

Ucayali Valley. Willard (1966: 69) reported that between 1924 and 1926, Bassler collected a few isolated 'Pliocene' fossils including *Anisothyris* (=*Pachydon*) as well as *Ampullina* and *Natica*, which are almost certainly misidentified. Willard also tentatively identified a large conical gastropod as *Itaborahia*, a possible member of the pulmonate Superfamily Bulimulacea (tree snails). The genus is known only by its type species in the alleged Miocene of Brazil (Zilch 1960: 485). If *Pachydon* is truly present, then the age is likely to be Pebasian rather than later (Pleistocene or Holocene as in the case of the Porto Peter locality in Brazil, p. 359, whose age was reviewed by Simpson, 1961).

Yarina. Upstream from Isla Navarra, close to Rio Huallaga. Boss & Parodiz (1977: 118, figs 10, 11) described, figured and dated as Eocene an unidentifiable member of the Thiaridae or Pleuroceridae as *Doryssa corrosensis* (Pilsbry & Olsson, 1935), originally described from the Palaeogene Los Corros Formation of the Magdalena Valley, Colombia. The Yarina fossil might be of any age between Cretaceous and Quaternary.

Yurimaguas. 5° 54′ S, 76° 05′ W on Rio Huallaga. At Santa Isabel on Rio Paranapura, to the west of Yurimaguas, Bassler collected (? in 1925) many examples of small species identified by Willard (1966: 70) as *Semisinus* (=*Hemisinus*) and *Anisothyris* (=*Pachydon*).

B. Brazil

Both the classic localities of Canamá (Brown 1879, Etheridge 1879) and Três Unidos (Oliveira & Carvalho 1924, Roxo 1924) are on the Peruvian (north) bank of Rio Javari, and not, as is often indicated, in Brazil: see above. Several Brazilian localities, whose faunas have not been fully described, are mentioned in *Projeto Radambrasil* (published as *Levantamento Recurs. Nat.*, by Departamento Nacional da Produção Mineral (=DNPM).) in which the results of a multi-disciplinary study by numerous authors are published. The volumes of most relevance to the Pebasian are **14** (Fernandes *et al.* 1977), **15** (del'Arco *et al.* 1977) and **18** (Lourenço *et al.* 1978). All the localities in question, whether their faunas are Pebasian or not, were treated by them as Solimões Formation. Some are dealt with in some detail below. Several of the more interesting are discussed in the section on **Três Unidos**, p. 329.

Aquidaba. 6° 30′ S; 69° 40′ W, on Rio Jurua; see under **Três Unidos**. It has yielded fossils once thought to be Pebasian, but is now shown to have a very different fauna (del'Arco *et al.* 1977).

Atalaia do Norte. 4° 20′ S, 70° 12′ W. Right (south) bank of Rio Javari, about 20 km upstream from Benjamin Constant. Costa (1980) redescribed and figured several gastropod species, all belonging to the Rissoacea, from the State of Amazonas, Brazil. The following few species were recorded from this locality. No bivalves were included. The full extent of the fauna is unknown.

original determinations	revised determinations
Hydrobia ortoni (Gabb)	*Dyris ortoni* (Gabb)
Hydrobia lintea (Conrad)	*Dyris lintea* (Conrad)
Liris minuscula (Gabb)	*Liris scalarioides* (Etheridge)
Dyris gracilis Conrad	*Dyris gracilis* Conrad
Lacuna (Ebora) crassilabris (Conrad)	*Eubora* sp. (*woodwardi* Kadolsky or *crassilabris*)
Pseudolacuna macroptera Boettger	*Toxosoma eborea* Conrad

The genera *Toxosoma* and *Eubora* and all the species listed above are endemic to the Pebasian. All appear to occur equally with both brackish- and fresh-water elements of the Pebasian fauna at other localities.

Canamá (see p. 327; Peru, *not* Brazil).

Fracoas (Cachoera das). See under **Três Unidos** (p. 329), mis-spelling of **Tracoás** in Roxo (1924).

Igarapé da Extrema. (* p. 331.) See also under **Três Unidos** (Igarapé = stream).

Ipiranga or **Ypiranga**. 2° 59′ S, 69° 35′ W, on right (south) bank of Rio Içá, State of Amazonas. Section referred to, without mentioning fossils (Oliveira & Carvalho 1924: 73, map and perfil 21). Fernandes *et al.* (1977: 49 *et seqq.* and map) show this locality as Solimões Formation, and they list (1977: 72) *Hydrobia, Lacuna, Pseudolacuna, Neritina, Congeria, Pachydon cuneatus* Conrad and *P. tenuis* Gabb, along with *Chara*, ostracods and fish teeth, which were collected by Oliveira & Carvalhos in 1919, now in Departamento Nacional da Produção Mineral (*Projeta Radambrasil*). This fauna appears to be typical of the Pebasian and indicates brackish conditions. *Mytilopsis* is frequently misidentified as *Congeria*. Ipiranga and São Paulo da Olivença are probably among the two most easterly localities from which Pebasian fossils have been recorded.

Jesumira, Acré Territory. A small tributary of the Mõa, which in turn flows into the Juruá just above Cruzeira do Sul. The record of *Pachydon* (Maury 1937) is almost certainly incorrect (see **Porto Peter**).

Jutaí, Rio. Series of vertebrate localities in river banks, approximately 150 km SE of Benjamin Constant (see **Solimões Formation** and **Três Unidos**).

Poreré. 3° 20′ S, 67° 30′ W (Purper 1977: 355, map). Costa (1980) described from boring CPCAN II *Hydrobia tricarinata* Boettger (=*Dyris tricarinata*), *H. lintea* and *Dyris gracilis*. These indicate that the fauna is Pebasian. Purper (1977: 354) described ostracods, one of which was subsequently named *Cyprideis purperi purperi* by Sheppard & Bate (1980: 99). Its type locality is Pichana and it is only known from the Pebasian. It is thought to be a brackish-water species.

Porto Peter, Acré Territory. Simpson (1961) demonstrated that the small molluscan and plant biotas described from here were not Pebasian, but came from an infilling of an oxbow lake of either Recent or very late Pleistocene age. Maury (1937) had described poorly preserved bivalves from here and from **Jesumira** (q.v.) as *Anisothyris ACREANA* sp. nov. and *A.* cf. *ovata* (Conrad) respectively. According to Dr Dwight Taylor (U.S. Geol. Surv.), whose opinion Simpson (1961: 622) quoted, these were quite likely to belong to the Corbiculacea (found in the living Amazon fauna). It should be pointed out, however, that some of the reasons they gave for rejecting these fossils as members of the genus *Pachydon* (= *Anisothyris*) of the Corbulidae are oversimplified: some species of *Pachydon* are equivalve and do not have prominent beaks. On the other hand the roughly circular outline of these fossils probably points to the Corbiculacea rather than the Corbulidae.

Quixito, Rio. 4° 29′ S, 70° 18′ W (* p. 329, with **Três Unidos**).

Rebeiros. Not in Gazetteer; situated on southern (Brazilian) bank of Rio Solimões, about 32 km below confluence with Rio Javari; see section on **Canamá** (p. 327) for reports by Brown (1879) of fossiliferous clays.

São Paulo da Olivença. 3° 27′ S, 68° 48′ W (Purper 1977: 355, map). Costa (1980) described from borehole CPCAN III a very similar fauna to that occurring at Atalaia do Norte (q.v. for redeterminations): *Hydrobia tricarinata, H. lintea, Liris minuscula, Dyris gracilis, Lacuna (Ebora) crassilabris* and *Pseudolacuna macroptera*. Purper (1977) described ostracods subsequently named by Sheppard & Bate (1980) as *Cyprideis purperi purperi* (see **Poreré**) and (1980: 101) *Otarocyprideis elegans*, which is also a brackish-water species whose type locality is Pichana.

Solimões Formation. Vast areas of the Amazon Valley in Brazil, from the Peruvian and Colombian borders to as far east as Manaus were mapped as Solimões Formation in *Projeto Radambrasil* (see head of this section). This was dated as Pliocene and Pleistocene. Some localities have yielded Pebasian molluscan faunas: Três Unidos, Atalaia do Norte, Poreré and Tamanduá are among those mapped as Solimões Formation. However, at other localities mapped as this Formation (Aquidaba, Porto Peter), the molluscan fauna appears to be more like that of the present-day Amazon region. The Solimões vertebrate faunas have never been found with Pebasian molluscs and may be of entirely different ages (see **Jutaí,** Rio).

Tamanduá. 3° 57′ S, 68° 10′ W (Purper 1977: 355, map). Costa (1980) described from boring CPCAN I three Pebasian gastropods *Hydrobia lintea, Lacuna (Ebora) crassilabris* and *Pseudolacuna macroptera* (see Atalaia do Norte for redeterminations). *Otarocyprideis elegans* is among the few ostracods known from there (see **São Paulo da Olivença**).

Tracoás or **Tracoá** (Cachoera da). (* p. 330). Incorrectly spelt as Fracaos in Roxo (1924). See also under **Tres Unidos** (Cachoera = waterfalls or rapids).

Três Unidos (*p. 329). On Peruvian bank of Rio Javari.

Ypiranga (see **Ipiranga**).

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